MOVEMENT ECOLOGY AND CONSERVATION: THE CASE OF AFRICAN VULTURES

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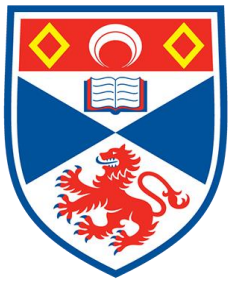

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Thesis presented to the University of St Andrews, in co-tutelle with the University of Aveiro. This work was carried out whilst enrolled in the Doctoral Programme of Biology and Ecology of Global Change, under the scientific supervision of Doctor Monique MacKenzie and Doctor Lindesay Scott-Hayward of the School of Mathematics and Statistics of the University of St Andrews, and Professor Fernando Morgado of the School of Biology of the University of Aveiro.

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To all the raptor enthusiasts!

Abstract

The movements of critically endangered vultures, equipped with satellite-based tracking devices in Namibia, were inspected using Generalized Additive Models. Models incorporated spatially adaptive (1D and 2D) smooths via the Spatially Adaptive Local Smoothing Algorithm (SALSA) and Complex REgion Spatial Smoother (CReSS) method. The correlated nature of geo-location data was address via robust standard errors.

The results of this thorough and integrative study of movement ecology have an unprecedented level of detail, far exceeding what is available in the literature. Namely, vultures were seen throughout Namibia and its five neighbouring countries with three individuals visiting locations farther than 1,000 km from where they were initially seen. Large variability was found both within and between birds. Differences were perceived in four daily movement properties, even though temporal differences were only captured for daily distance travelled (monthly) and daily maximum displacement (seasonally). There was noticeable variation in the size of the areas each bird used from month to month, often showing very little spatial overlap. Home ranges varied greatly; one bird expanded its monthly home range as much as nineteen times its smaller size. Contrastingly, core areas remained sometimes constant. Home ranges were three to five times larger than the respective core areas, clearly indicating a non-uniform use of the environment. The extensive study area (2.3 million sq.km) was characterised using habitat features, climate conditions and indices of human presence. Vegetation index, minimum distance to river and minimum distance to road were consistently important in explaining the probability of bird presence. Nonetheless, each vulture used its environment in its own way.

These novel findings support trans-frontier conservation measures, represent crucial support to revise the geographic extent of existing conservation actions and constitute the basis to predict the risk of exposure of vultures to lethal threats or to assess changes under Climate Change scenarios.

Declarations

Candidate's declaration

I, Cláudia Estevinho Santos Faustino, do hereby certify that this thesis, submitted for the degree of PhD which is approximately 59,00 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree.

I was admitted as a research student at the University of St Andrews and at the University of Aveiro (Portugal) in May 2015 as part of a joint programme.

I received funding from an organisation or institution and have acknowledged the funder(s) in the full text of my thesis.

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A few years ago I fell in love with a map. No, really! The incredible amount of information so beautifully summarised in that map – it's unbelievable! And so I wanted to learn how to make such map. Thank you Monique, for agreeing to supervise me, for being so patient through all the funding applications, and for all the mentoring. I've learnt so much! And I now know how to make *that* map!

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1 General Introduction

This thesis explores aspects of the ecology of movement of free-ranging wild animals. Understanding how animals move not only extends our knowledge on how wildlife interacts with its surrounding environment, but it also provides crucial information to assist with the conservation of a species. This chapter introduces animal movement and investigates the drivers that shape its patterns. The ability to interpret animal movement is growing alongside the improvements in data collection and analytical tools. These topics are discussed in this chapter, and a link is made to the conservation of vultures. Lastly, this chapter includes motivations for this thesis along with the thesis outline.

1.1 Movement Ecology

How, why, when and where do animals, plants and microorganisms move? These questions have long been the subject of human curiosity and have motivated research in diverse fields. A decade ago, an integrative approach was proposed to unify the study of movement of all organisms and it was termed "movement ecology" [1]. This working framework is based on the interaction between four basic components; three are based on the organism itself: the internal state (why move?), motion (how to move?), and navigation (when and where to move?); and the other relates to the external factors affecting the movement [1].

The movement of an organism can be defined as a change in its spatial location in time [1]. Movement plays a major role in determining the fate of individuals, the structure and dynamics of populations and communities; it acts across multiple spatial and temporal scales. Movement facilitates many vital ecological processes, namely mobile organisms disperse pollen, seeds, and diseases. These processes are economically important with links, for example to the production of goods of value to humans such as crops which are valued at hundreds of billions of dollars per year [2]. Animal movement thus provides essential insights into patterns of biodiversity and ecosystem function [3].

Movement reflects a dynamic interplay between both internal and external factors to the individuals [1]. Internal factors include hunger, thirst, fear; external factors include habitat structure and locations of key resources, predators and enemies [4]. At play are also social interactions that lead to group dynamics, and territorial behaviour associated to reproduction strategies [5]. The need to obtain food and other essential resources drives various ranging movements also referred to as foraging [4].

The geographic area utilised by an individual for all normal activities, linked together through animal movement is often termed a “home range” [6]. In order to meet the full range of physiological and ecological requirements of an individual over an extended period, a suitable home range typically must have an adequate supply of food and water, shelter, breeding sites, and often locations which are adequately secure against predators and parasites [6]. Both the habitat and internal state of animals might change through time and cause home range size to vary [7]. Species will differ in movement strategy, with some species extending over a large area each year [6]. Given this movement variation, it is convenient to consider whether patterns of movement are repetitive (i.e. if there is a tendency to return to places visited before or the converse) and whether movements of multiple individuals are coordinated [6]. A migratory movement is described by a cyclical pattern in which individuals move between two or more non-overlapping home ranges at different seasons of the year. In turn, nomadism occurs when individuals show unpredictable patterns of movement among multiple non-overlapping home ranges. Alternatively, animals whose movements fall within a single (contiguous) boundary all year long are termed residents [6].

While much empirical evidence exists regarding the variability of movement strategies between different species, evidence is somewhat less prevalent for the extent of variability of movement strategies within a species [5, 8, 9]. Movement behaviour may be driven by intrinsic differences in physiological factors, morphology or even personality affecting, for example, activity, boldness and exploratory behaviour [7]. Consequently, individuals in many species can adapt to varied environments and adjust behavioural strategies to facilitate resource acquisition through time [8]. Intraspecific variation in movement strategies may be particularly prevalent in environments in which resources are highly variable, as individuals that can learn when and where to access the best resources and alter their movement strategies accordingly will be those most likely to survive and reproduce [8]. Partial migration, where populations are composed of a mixture of migratory and residential individuals is widespread, with examples across all major vertebrate groups, namely in large raptors [8]. For example, the movement ecology of Pyrenean bearded vultures (*Gypaetus barbatus*; France, Spain) is distinct between territorial and non-territorial individuals [10]. Wheat *et al.* explored variation in movement patterns in more detail [8]. The authors found that bald eagles (*Haliaeetus leucocephalus*; Alaska (USA) and Canada) exhibit strongly individual movement in terms of travel pathways and locations visited throughout the year, with consistent general movement patterns within strategies. Four patterns of movement were described: breeding individuals, largely sedentary and remaining near nest sites year-round; non-breeding migratory individuals, with regular seasonal travel between northern summer and southern winter ranges; non-breeding localised individuals that displayed fidelity to foraging sites; and non-breeding nomadic individuals with

irregular movement. Non-breeding migratory adults are often present in raptor populations and are known as floaters. Floaters may have to sacrifice access to seasonally abundant resources in distant locations in favour of holding nesting territory outside the breeding season, as territorial pairs occupy all suitable nesting habitat [11].

Quantifying individual variability in movement behaviour is also critical to our understanding of population-level patterns in animals [8]. Behaviour has an important effect on the viability of a population since the strategies chosen by individuals influence demographic parameters such as dispersal, survival and reproduction [12]. Identifying individual movement strategies can thus help researchers understand the flexibility with which animals can respond to variable environmental conditions and design more effective conservation management plans [8].

1.2 Measuring animal movement

Even though the study of animal movement has a long history, much has changed with more recent advances in tracking technology. Electronic devices (commonly referred to as "tags") equipped with Global Positioning System (GPS) have been used for several decades to monitor the locations of wild animals [3, 13]. A tag is attached to an animal (e.g. a collar) and its geo-referenced locations are recorded at subsequent time points. The pioneering automated tracking tags used the Argos satellite network but these were expensive and the accuracy of their measurements varied greatly [14]. The coverage of global migration of larger species was possible, but with low-accuracy (±500 m up to ± 1,000 km) fixes recorded only once every few days [14]. Technology moved on and nowadays it is possible to receive data in real time; the dimensions of the devices have also decreased immensely increasing the utility of tags in ecology. Current GPS tags powered with solar panels on migrating birds can send estimates of location recorded every second, and those locations can be transmitted in real time using the mobile phone network [14].

Improvements in battery duration were also decisive, making it possible to reduce the time interval between data points as well as extend the duration of the data collection [15]. The duration of the battery needs to be balanced with the sampling frequency and it is usually guided by the aim of the study. High-frequency data will allow the assessment of small-scale behaviour while studies of long duration will document the spatial extent of habitat use. Lastly, even though the main goal of most animal tracking studies is the inspection of their geo-referenced locations, electronic devices

nowadays are also equipped with other sensors to help monitor not only the animal but also its environment [3]. Three-axial accelerometers for example, built into the tags, can be used to describe continuously the behaviour and energy consumption of the animal by measuring fine-scale body movements [16].

Not surprisingly, technological advances have raised the dimension of animal movement data sets to that of "big data" and the increases in data volumes are expected to continue [3]. Descriptive statistics or visualisation tools may be sufficient to address the simpler questions in movement studies. Nonetheless, more sophisticated statistical methods have been developed to interpret the large volume of information made available [17-20]. The multitude of methods offered can make the choice of a particular approach an arduous task, more so for ecologists and wildlife biologists with less statistical training [17]. The Generalized Additive Model (GAM, [21]) is one approach to model complex structures in ecological data, with wide applications and extensions [19, 22]. However, no single method has yet stood out prominently from the animal movement modelling options [18]. Each new statistical framework for analysing telemetry data brings potential for new inference and new insights into the understanding of the processes underlying movement ecology.

1.3 Species conservation

In 2002, world leaders committed, through the Convention on Biological Diversity (CBD), "to achieve by 2010 a significant reduction of the current rate of biodiversity loss" [23]. Acknowledging the impact of biodiversity loss on human well-being, the "2010 target" has been incorporated into the United Nations Millennium Development Goals [24]. Nonetheless, an assessment of the indicator set out by the CBD showed that overall no significant reductions in rate of biodiversity declines at the same time as the indicators of pressures on biodiversity showed increases [25].

Furthermore, approximately up to 70% of the land surface on Earth is currently modified for human activities [26]. As a consequence, changes are being perceived worldwide in the patterns of biodiversity and ecosystem functions [27]. The escalating footprint of human activities is triggering the loss of habitat and biodiversity, but is also affecting the way animals move through disturbed habitats [28]. On average, the movements of mammals in areas with higher human footprint were one-half to one-third the extent of their movements in areas with a low human footprint [28].

Not all species have the same importance in maintaining ecosystems resilience [29]. Species groups also have widely dissimilar population statuses and trends [25]. Vultures are the sole obligate scavengers and as such, a unique functional group among vertebrates which play an unparalleled role in maintaining ecosystem balance [30]. Along with predators, scavengers are considered keystone species (i.e., one that plays a unique and crucial role in the way an ecosystem functions), and are often seen as ambassadors for ecosystems health [31]. Two key ecological roles which are well established in the literature describe predators exerting top-down pressures on prey communities, and that of scavengers consuming large amounts of carcasses and organic waste. They also provide crucial benefits in human landscapes, such as disease regulation through host density reduction, increasing agricultural output through elimination of species that destroy crops, and waste disposal services [31]. For instances, the ability of *Gyps* vultures to rapidly locate and consume dead ungulates keeps the environment clean of carcasses and other organic waste (such as decaying food matter), with potential ramifications for the spread of diseases in both wild and domestic animals, as well as for the control of pathogenic risks to humans [32]. Also, Egyptian vultures (*Neophron percnopterus*), have been reported to remove livestock and human faeces that would otherwise cause water contamination around the towns and villages of Socotra (Yemen; [33]).

Despite their ecological importance, vultures are among the list of species considered most threatened with extinction [30, 31]. A recent review has shown that raptors are particularly threatened, and more so the Old World vultures [34]; Old World vultures are vultures that are found in the Old World, i.e. the continents of Europe, Asia and Africa. A recent prioritization analysis of conservation areas based on factors such as risk, indicated a concentration of highest priority areas for vulture conservation in southern Africa [35]. Also, 18% of raptors are threatened with extinction and the populations of 52% are declining globally [34]. Two of the most serious threats to African vultures are food shortages caused by improved animal husbandry and over-harvesting of wild ungulate populations, and mass poisoning when they consume carcasses laced with poisons intended to kill predators of livestock [36]. Their gregarious feeding behaviour and ability to forage over large areas make *Gyps* vultures particularly susceptible to mass poisoning events which tend to occur most frequently on farmland with no conservation protection status [37]. For example, increasingly frequent poisoning incidents are the most likely cause of a 52% decline in *Gyps* vulture numbers in the Masai Mara ecosystem (Kenya) over a 30 year period [36]. And those poisoning events do not cease to happen – just this June (2019) “more than 530 endangered vultures have been killed in northern Botswana”, making it to the international news [38].

Several studies have found that vultures are becoming increasingly restricted to protected areas in different regions of Africa and the importance of protecting them beyond the boundaries of wildlife reserves is considered vital to their future conservation [32, 35, 36, 39]. The need to implement effective conservation measures is imperative. A Multi-Species Action Plan to Conserve African-Eurasian Vultures has been formalized [32]. The Action Plan puts forward measures to halt the current population declines [32] and brings these species to the top of the international conservation policy agenda [35]. Among the set objectives and recommendations from the Action Plan are:

"To ensure availability of suitable habitat for vultures to nest, roost and forage"; and

"To support vulture conservation through crosscutting actions that contribute to addressing knowledge gaps".

1.4 Motivation and thesis overview

It is as critical, as it is urgent, to extend the knowledge about mobile wildlife, as well as to inform effective conservation plans for endangered species. An ongoing monitoring project in Namibia has been collecting information about two critically endangered raptor species. Such monitoring is generating a wealth of information that has allowed the description of movement patterns of these species, in an unprecedented way. Prior to this study, the majority of literature available on white-backed and hooded vultures addressed aspects of population biology and status. Those studies that incorporated movement have focused mostly on energetics and nesting with only four studies describing movement patterns beyond this (see description and maps collated in **Appendix I**).

This thesis explores movement ecology to address the call for action and to fill existing knowledge gaps in the movement ecology of African vultures. Specifically, the movement of seventeen white-backed and hooded vultures, equipped with satellite-based transmitters, were studied to aid their conservation.

Chapter 2 starts by introducing the study species, presenting relevant biological and ecological information about the African white-backed and hooded vultures. A description of the study site where the satellite-based transmitters were deployed, and the field protocols is also given. The chapter closes with a detailed description of the main methodologies implemented in the thesis, both

extensions of the linear model - Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs).

Chapter 3 focuses on movement patterns of vultures at a daily scale. Four properties of movement are investigated: daily distance travelled, daily maximum displacement, daily overall displacement, and straightness of a daily path. Descriptions are made for each of the birds and temporal changes are assessed. Patterns in the daily movement are analysed both separately and in combing properties, and groups of birds are contrasted to illustrate the biological relevance of some of the findings. Here, the *travellers* and *locals* are introduced.

Chapter 4 focuses on the patterns of monthly range areas utilised by vultures. Preferential areas are identified and both home ranges and core areas are presented with associated uncertainty measures. A description is made of the estimated size of those range areas as well as for the ratio of core area to home range for each bird. Temporal changes are assessed, individually and in combination. Selected birds are contrasted to highlight the flexibility of the movements displayed. The variation in the monthly range areas is also examined in terms of its shape and geographic extent. Maps are presented for each vulture and contrasting examples are discussed. Lastly, two birds are compared to illustrate a potential biological significance and the *floaters* are introduced.

The third data chapter (**Chapter 5**) is motivated by the characteristics of the habitat each vulture utilised. It begins with a characterisation of the study area based on environmental covariates (habitat characteristics, climate variables, and human presence). Then the habitat preferences are modelled for each vulture individually, incorporating also a temporal (bird-month) and a spatial (geographic coordinates) term. The importance of the environmental covariates is discussed for each vulture with special relevance on the biology and conservation of the species. Namely, birds are contrasted to illustrate the range of exposure to varying environments. The importance of each of the environmental covariates for each vulture is illustrated and compared. Lastly, predictions are mapped showing the seasonal distribution for each bird.

The thesis concludes with a general discussion of the main findings in light of their biological and ecological significance (**Chapter 6**). The findings and outputs generated from this thesis have sound statistical support and direct application in both conservation and management actions. Those applications are discussed as well as prospects for future work.

2 Methods

The work presented in this thesis was built on information gathered from satellite transmitters deployed on two critically endangered species of vultures in Namibia. Relevant details about the study species and the data collection are presented in this chapter. Also, the theoretical grounding for the methods implemented throughout the thesis is described. Additional specific detail is given in each data chapter.

2.1 Study species

The focal species of this study was the white-backed vulture (*Gyps africanus* Salvadori, 1865; Figure **2**-**1**). This is the most common and widespread vulture in Africa. African white-backed vultures are native to Namibia and surrounding countries. The global population of this species has been estimated at 270,000 individuals [40] (Figure **2**-**1)**. It has nonetheless been declining severely having incurred a 90% drop over three generations in parts of its range [41]; it is consequently listed as Critically Endangered by the International Union for Conservation of Nature (IUCN) [40]. This vulture is primarily a lowland species of open wooded savannah, particularly in areas of *Acacia*, and requires tall trees for nesting [40]. White-backed vultures feed by scavenging from carcasses of medium to large mammals, including domestic livestock, and they are most often seen circling together above food and feeding in large noisy flocks at large carcasses [42]. Their energy efficient soaring flight, keen eyesight and social foraging behaviour enable them to locate sparsely and unpredictably distributed carcasses over a large area, often before their mammalian competitors [39]. This species soars up to 800 m in thermals, gliding between thermals at up to 65 Km/h [42]. They are gregarious, congregating at carcasses, in thermals and at roost sites [40]. Some populations are thought to shift their ranges in response to food availability and seasonal rains [32].

African white-backed vultures are present in all but the treeless areas of Namibia. Areas of higher density in Namibia include the Etosha National Park and the Zambezi Region (Figure **2**-**1**). They are also relatively common throughout the central and eastern parts of the country [42]. Following a long term monitoring and ringing research project in Namibia, these vultures are known to breed during the winter with eggs which are laid mostly around May although with regional variations [43]. The study shows eggs were laid between March and July in Etosha (1998 -2012, n=345); and between April and June for the central regions (2003-2013, n=347). Also, both birds in a breeding pair share the

parental care [44]. Namibian population estimates suggest this species occupies an area of 305,000 sq.km [42] with up to 5,600 pairs, which can be found at a density of 3.8 nests/10 sq.km in a colony near the Waterberg Plateau [42].

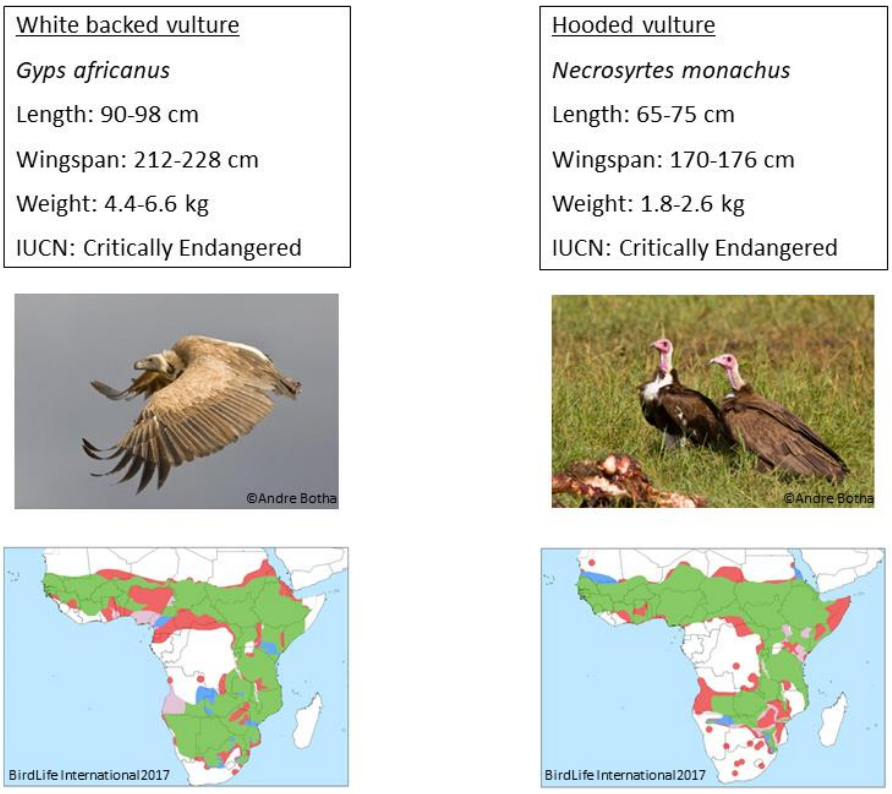


Figure 2-1 Details from the two species of vulture included in this study. Distribution map showing: resident (green), non-breeding (blue), probably extinct (pink) and extinct (red). Conservation status as defined by the International Union for Conservation of Nature (IUCN). Sources [40, 44-46].

Additionally, this study also included the hooded vulture (*Necrosyrtes monachus* Temminck, 1823; Figure **2-1**). This species is widespread in sub-Saharan Africa from Senegal southwards to northern Namibia and Botswana, also found in Zimbabwe and north-eastern South Africa [45]. Hooded vultures have a smaller population size than the white-backed vultures, estimated to a maximum of 197,000 individuals [45]. Hooded vultures are also experiencing rapid decline, with a potential drop in 83% decline (range 64-93%) over three generations [41]. Such decline supports its IUCN conservation status of Critically Endangered [45]. This species occurs in a range of habitats, namely open grassland, forest edge and wooded savannah [45]. Hooded vultures may occur at higher densities in areas where populations of larger *Gyps* vultures are low or non-existent [45]. Hooded vultures are generally sedentary, with some dispersal by non-breeders and immature birds. Also, movement has been related to rainfall in the Sahel of West Africa [45].

Hooded vultures feed mainly on carrion. They also take insects and can congregate in large numbers during insect emergences [45]. In West Africa and Kenya, they breed throughout the year, but especially from November to July. Breeding in north-east Africa occurs mainly in October-June, with birds in southern Africa tending to breed in May-December [45]. The species has been confirmed to breed in Namibia but there is insufficient information to derive laying dates [43]. They nest in trees and are known to favour *Ceiba*, such as Kapok tree, in Senegal [45].

2.2 Field protocol

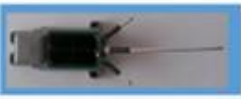
Tracking devices were fitted to 17 wild vultures between February 2015 and November 2017. Deployments were made mostly from Etosha National Park (11), one device was deployed in the Kunene Region (West of Etosha) and the remaining five, from Bwabwata National Park (**Figure 2-2**).

Birds were captured at multiple sites and briefly trapped with foot-hold traps. Foot-hold traps were used on the majority of cases where the traps were buried under the earth and camouflaged next to a bait carcass. Bait was usually a carcass of a medium size herbivore (e.g., springbok, zebra, blue wildebeest) found dead of natural causes. An air-propelled net-gun, rather than foot-hold, was used on two occasions, baited with a buffalo that died of natural causes. Adult birds were targeted during the capture process to minimise any effects of transmitter on their welfare; birds were aged according to the South African Bird Ringing Unit (SAFRING) protocol [47].

Figure 2-2 Southern African countries, and locations where tracking devices were deployed (blue dots). Deployments were made from Etosha National Park (in light brown, Central North of Namibia), the Kunene Region (West of Etosha) and Bwabwata National Park (in light brown, Northeast of Namibia in the Zambezi Region).

Once caught, the birds were carefully released from the trap and moved to a safe location to be handled. Patagial and metal rings were fitted, and biometrics were noted (age, mark, condition, weight and dimensions) according to the SAFRING protocol [47]. Additionally, solar-powered Global System for Mobile Communication /Global Positioning System (GSM/GPS) transmitters were attached using leather (and occasionally Teflon) harnesses. Four types of transmitters from different providers were used, each differing slightly in its specifications (**Figure 2-3**). Namely, the transmission rate was one location per hour for the Savannah tags (http://www.savannahtracking.com/), one location every 10 min for CATS (http://www.cats.is/), and one location every five minutes for the E-obs (https://www.e-obs.de/) devices.

Vultures are listed under CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora, https://www.cites.org/) under Appendix II. Therefore, any potential trade must be controlled against over-exploitation and only certified professionals can handle these species. All animal handling was carried out under valid research permits, mostly by G. Shatumbu who holds an official Bird Ringing Licence SAFRING No: 1477 emitted by the Ministry of Environment and Tourism, Namibia.

			
Producer Number	Savannah (7)	CATS (1)	E-obs (9)
GPS	√	√	√
Altitude	-	√	√
GSM/GPRS download	-	√	√
Satellite download	√	-	-
Upload of new settings	√	-	√
Speed	-	-	√
ACC	-	-	√
Temperature	√	-	√
UHF Ping	√	-	√
Weight		53g	48g
Mortality alarm	Good	Poor	Poor

Tag ID	Producer
5215	E-obs
5403	E-obs
5404	E-obs
5784	E-obs
5785	E-obs
5786	E-obs
5787	E-obs
5788	E-obs
5789	E-obs
CAT1	CATS
st2010-1330	Savannah
st2010-1332	Savannah
st2010-2607	Savannah
st2010-2608	Savannah
st2010-2609	Savannah
st2010-2697	Savannah
st2010-2700	Savannah

Figure 2-3 Details of the transmitter used in the study (left hand side; adapted from image provided by O. Aschenborn) and corresponding tag ID. Tag ID for White-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

2.3 Study site

Field work was conducted from three areas in the North of Namibia (**Figure 2-2**). Most deployments were made in the plains surrounding Okaukuejo (located inside Etosha National Park, where most blue dots are shown in **Figure 2-2**). The vegetation in Etosha varies from arid to semiarid savannah and supports a vast variety of wildlife [48]. One deployment was made in the Kunene Region, bordering Etosha National Park to the west. The remaining five deployments were carried out within the Bwabwata National Park at the far Northeast of the country. This park comprises of low vegetated sand dunes with the Okavango River in the west and the Kwando River in the east. The wildlife in this location is also very rich [49].

Namibia has an average of 300 days of sunshine annually with an arid climate. The weather can be largely described as hot and dry with regions showing considerable differences regarding precipitation and temperature. The summer takes place from October to March with temperatures and rain increasing; the main rainy season starts in January when the vegetation turns markedly green. During the winter (June to September) the rain stops and temperatures are moderate during the day but routinely cold at night. In winter the vegetation typically turns brown in colour [50].

Droughts are not uncommon in southern Africa, and can generate acute local socio-economic impacts [51]. Exceptionally dry conditions were experienced across southern Africa during the austral summer wet season of 2015/2016. That was the most intense drought in the 116-year historical record and

several countries declared national drought emergencies (including Botswana, Namibia, South Africa, Lesotho, and Zimbabwe). Southern Africa is currently experiencing yet another severe drought and countries such as Namibia have recently declared a state of emergency [52].

Throughout this thesis, seasons were defined as: "hot wet" between January and May, "cold dry" between June and August, and "small rain" between September and December (Pierre Du Preez, *pers. comm.*). This definition was made based on the conditions present at Etosha National Park, where the majority of deployments took place. Nonetheless, vulture locations were recorded not only throughout most of Namibia but also over its five neighbouring countries (Angola, Zambia, Zimbabwe, Botswana and South Africa; see **Figure 3-1** in **Section 3.2.1**).

Figure 2-4 and **Figure 2-5** show the variation of temperature and precipitation across the study area. These figures were produced using the environmental data extracted for each of the vulture locations throughout the entire study area (see full details on **Sections 5.2.2** and **5.2.3**; see also **Figure VII. 5** and **Figure VII. 6** in the Appendix for further detail).

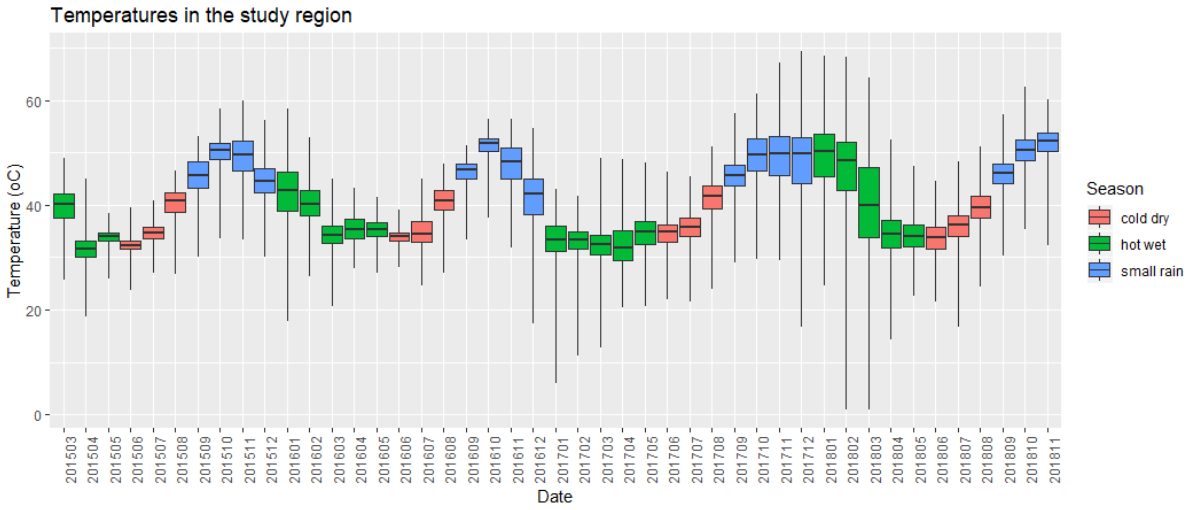


Figure 2-4 – Temperatures (°C) recorded throughout the study region, during the time period vultures were monitored in the present study. Monthly temperatures are shown in each box plot with the 25% (bottom), 50% (middle) and 75% (top) quantiles, as well as the minimum (extent of the lower line) and maximum (extent of the upper line) values. Colours represent seasons: light red – cold dry, green – hot wet, blue – small rain.

There was clear temporal variation in both temperature and precipitation. Despite its name, the hot wet season did not produce the hottest temperatures however, it did have the highest variability in temperatures of all the seasons and the highest rainfall. The cold dry season presented a slight increase in mean temperatures and the drastically driest weather. The small rain season generally had

the highest mean temperatures and only a few months with rain. The wide range of values in each month are not unsurprising as the study area is very large. There is a more detailed characterisation of these variables in **Section 5.2.3**.

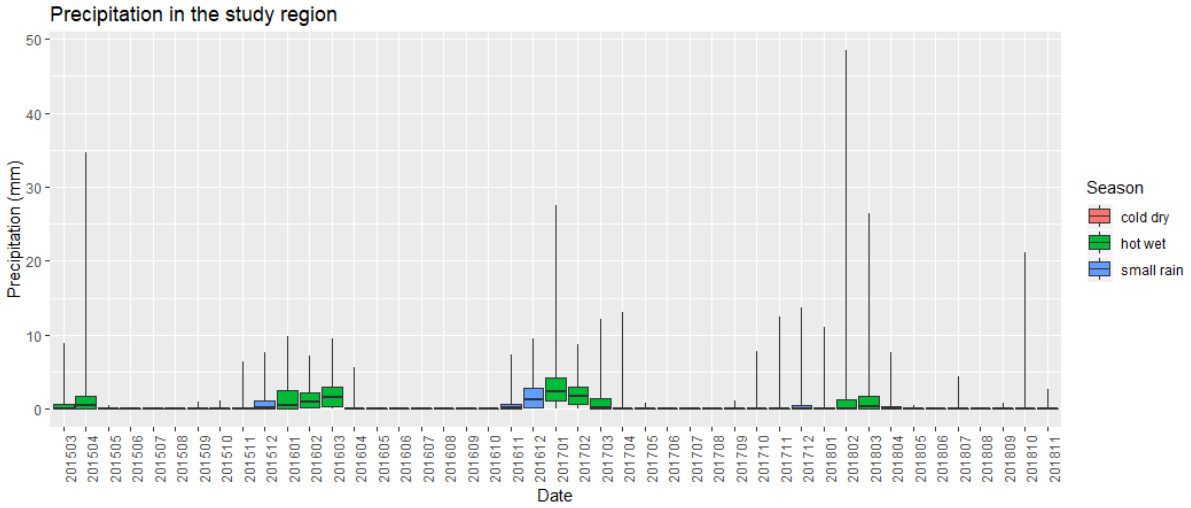


Figure 2-5 – Precipitation (mm) recorded throughout the study region, during the time period vultures were monitored in the present study. Monthly temperatures are shown in each box plot with the 25% (bottom), 50% (middle) and 75% (top) quantiles, as well as the minimum (extent of the lower line) and maximum (extent of the upper line) values. Colours represent seasons: light red – cold dry, green – hot wet, blue – small rain.

2.4 Statistical methods

The methods implemented in this thesis are extensions of the linear model. Varying degrees of non-linearity are permitted when relating the response variable to one or more explanatory variables, and Generalised Linear Models extend linear models via the inclusion of a monotonic "link function" (GLMs, [53]). These models allow the response to come from a wide family of distributions, and do not necessarily assume that the data, given the model, are Normally distributed. This flexibility was particularly important when modelling the properties of daily movement appropriately, in **Chapter 3**. Specifically, some of the daily properties modelled are distances, which are strictly positive response values. So, whilst these values are continuous like the Normal distribution, negative values are not allowed. For this reason, it was decided that these distances are better described by a Gamma distribution-based model which is appropriate for data which is continuous and bounded by zero.

Generalised Additive Models further extend the flexibility between the response and explanatory variables with the use of "smooth terms" (GAMs, [21]). A smooth function of an explanatory variable can be incorporated into the model structure; bivariate smooth functions can also be implemented to

express interactions between two explanatory variables and the response. These characteristics increase the model complexity as well as the computational cost, but can prove extremely beneficial in describing heterogeneous patterns of the response variable appropriately. **Chapters 4** and **5** relate to the way vultures use their habitat (in a non-homogeneous way) and GAMs with a bivariate smooth function of the geographic coordinates (i.e., latitude and longitude) are implemented.

To better interpret the results presented and discussed in this thesis, it is important to understand the structure of these methods. The aim of this section is to describe the main components of GLMs and GAMs.

Generalised Linear Models

The basic structure of a Generalised Linear Model (GLM) includes a monotonic "link function" that allows the model to be specified in terms of a "linear predictor" [54]. The link function relates the mean of a response to a linear combination of one or more explanatory variables (or covariates, [19]). A GLM allows for a degree of non-linearity in the model structure, and also allows the distribution of the response to be according to some exponential family distribution (e.g. Poisson, Exponential, Gamma, Binomial, Gaussian) [54]. The exponential family distribution includes several distributions that are useful for practical modelling, such as the Poisson (for responses that represent non negative counts), Binomial (for successes from trials) and Gamma (strictly positive real responses) distributions [19, 54]. The basic formulation of a GLM is very similar to that of linear models, with the addition that a link function and distribution must be chosen [54]. In fact, the linear model is a special case of the GLM where the family is Gaussian with an identity link function.

In a situation where there are n observations from the response variable ($Y_i,\ i = 1, \dots, n$) and p covariates ($x_k,\ k = 1, \dots, p$), a GLM can be represented as:

$$g(\mu_i) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_p x_{pi}$$

where $\mu_i \equiv E[Y_i]$ (i.e., the expected value of the response data Y_i), $g(\cdot)$ is a monotonic link function, each β is a model coefficient and $Y_i \sim$ *some exponential family distribution*.

Using the Gamma distribution as an example (used in **Chapter 3** for the strictly positive distance measures), the GLM can be described as follows:

* the response Y is assumed to comes from a Gamma distribution and so $Y \sim Gamma\ (k, \theta)$, where k is a shape parameter and θ, a scale parameter;

* k is treated as fixed and known while θ_i is to be estimated,

$$E[Y_i] = \mu_i = k\ \theta_i \text{ and}$$

$$Var(Y_i) = \varphi\ Var(\mu_i) = {}^{1}/_{k} * k^2\theta_i^2 = k\theta_i^2,$$

where dispersion parameter, φ, is the reciprocal of the shape parameter $\varphi = {}^{1}/_{k}$;

* the linear predictor is $\eta_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_p x_{pi}$; and

* the link function $g(\cdot)$ chosen is the log, which ensures the outcome is non-negative,

$$g(E[Y_i]) = \log(E[Y_i]);$$

then, the resulting GLM can be represented:

1. in terms of the response as: $y_i = e^{\eta_i} = e^{\beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_p x_{pi}} + \epsilon_i$; or

2. on the scale of the log link function as: $g(E[Y_i]) = \log(E[Y_i]) = \eta_i = \beta_0 + \beta_1 x_{1i} + \cdots + \beta_p x_{pi}$.

While GLMs can accommodate some degree of nonlinearity between the relationship for each covariate and the response, this is determined solely by the link function and is relatively inflexible in practice. In many cases, more flexibility than GLMs provide is needed and GAMs are a reasonable alternative.

Generalised Additive Models

The key feature of Generalised Additive Models (GAMs) is that the mean of the response depends on the explanatory variables through a sum of "smooth terms"; each smooth term is a function of one or multiple covariates [55]. GAMs are an extension of a GLM where the linear predictor may describe a smooth non-linear function of the mean of the response; the response may follow any exponential family distribution, or simply have a known mean-variance relationship [54]. Generalised Additive Models can take the form:

$$g(\mu_i) = \alpha_i + f_1(x_{1i}) + f_2(x_{2i}, x_{3i}) + \cdots + f_q(x_{p-1i}, x_{pi}),$$

where $\mu_i \equiv E[Y_i]$ (i.e., the expected value of the response data Y_i, $g(\cdot)$ is a link function, α_i represent any strictly parametric model component, and each f_j $(j = 1, 2, \dots, q)$ is a smooth function of the (one or more) covariate(s) $(x_k,\ k = 1, \dots, p)$ [55].

This additional flexibility comes at the cost of two additional considerations. It is necessary both to represent the smooth functions in some way and to choose how smooth they should be [54]. The smooth functions are constructed from "basis" functions, which define the group of functions that collectively cover the whole range of the predictor data and give an appropriate curve for the data [54]. One basis function commonly used is the B-spline firstly introduced by de Boor (1978, [56]; [57]). B-splines consist of polynomial pieces, joined at certain values of the covariate, the "knots". Once the knots are given, the B-spline can be computed recursively, for any desired degree of the polynomial. A B-spline of degree 2, for instance, consists of quadratic pieces [57]. The higher the degree, the more flexible the function can be (degree 2 and 3 are most common). Furthermore, B-splines are "locally defined" since a polynomial piece is active between the two respective knots and is zero elsewhere [57].

In this thesis, the methods used are pure regression splines, as opposed to penalised regression splines or smoothing splines. Therefore, the choice of how smooth the splines should be, involves two crucial challenges: the selection of both the number and the location of the knots [57]. In contrast to regression splines, penalised splines use many more knots than would (typically) be required but the function wiggliness is controlled using a penalty function, chosen by an objective function or the user. Smoothing splines take this automation even further and assign each unique x-value a knot and rely entirely on a pre-determined penalty to control the wiggliness. Regardless, both the penalised spline and smoothing spline approaches allocate their knots regularly, making it difficult to capture functions with unusual shapes, thresholds and/or with abrupt changes in shape.

For all smoother based methods, too many knots lead to overfitting the data with a highly flexible function, while too few knots result in a model that is too smooth and leaves genuine patterns in the prediction errors. Additionally, the location of the knots is important to allow spatial adaptability in the smoothness of the resulting function. Knots can be allocated in a simple way, evenly spaced throughout the range of the predictor data or at quantiles of the distribution of unique data values [54, 58]. But other automated and data-driven methods can also be applied (e.g. [59]).

Several computational procedures for optimising the amount of smoothing have been proposed. One such procedures for univariate smooth terms is the Spatially Adaptive Local Smoothing Algorithm (SALSA, [59]). This smoothing algorithm automatically varies the number and location of knots in the model. It uses an adaptive knot-selection approach, accommodating local changes in smoothness. SALSA fits within the GAM framework and makes adaptive decisions based on Pearson residuals; knots are placed at locations where residuals are higher and fitness improvements are assessed. The algorithm combines a local-search strategy with a restricted forward/backward regression approach significantly reducing the number of models evaluated at each iteration [59].

In this thesis, B-splines with SALSA selection were used for univariate smoothing, however an extension of this approach was necessarily used for a bivariate smooth of the spatial coordinates. Continuing with the theme of regression splines, the Complex Region Spatial Smoother (CReSS, [60]) radial basis function was used alongside SALSA 2D for smoothness selection. CReSS was developed to deal with complex topographies such as fences or coastlines (e.g. [22]) and does this by employing geodesic (rather than Euclidean) distances between points. The smoothing method is also spatially adaptive owing to the choice of the size of the radial basis and as such it can accommodate any particularly patchy trends and target any local surface features. CReSS has recently been complemented by the addition of SALSA-2D for knot selection [22]. Previously, smoothness was achieved by model averaging with different knot numbers [60]. The MRSea package [61] available in the statistical software R [62], enables fitting of these CReSS-SALSA2D models also allowing the choice of either the exponential radial basis function or the Gaussian basis, which is the default. This smoothing method has found application in ecological studies such as: mapping the distribution of endangered species to inform spatial conservation planning [63], assessing the effects of human activity on wildlife [64], and estimating the density and distribution of wide ranging species using novel approaches [65]. In the analysis of vulture data, the complex topography aspect of this methodology is of little use as there are no known areas where the vultures cannot travel, i.e. areas that might be considered exclusion zones. Therefore, the method in this thesis employed Euclidean distances between points.

The MRSea package also contains an automated model selection procedure using cross-validation, which is more computationally efficient and better at describing unusual spatial patterns observed in the data, compared with the original CReSS with model averaging method. The addition of SALSA-2D has already proved crucial in teasing out detailed patterns of wildlife distribution with potential implications in wildlife management of Etosha National Park [22].

Models based on presence and absence data

Models used to describe species distribution have been shown to be effective when based on data with both the presence of the species and the environmental conditions available in the area [66]. It is also important to consider in these models where the animal *is not* – there are often environments characterised by unsuitable covariate ranges which are accessible to the animals but are not visited. Those points can be referred to as background data. Confirmed absences based on an entire population of animals is impossible to obtain for mobile species occurring in remote areas, but for those which are tagged, absence data can be reliably created. Those data can be referred to as pseudo-absences.

There are several options available to generate pseudo-absences, with a few studies comparing model performance based on that aspect [67, 68]. There is, however, no current consensus on how and where to sample such pseudo-absences, or how many [67]. One option is to generate pseudo-absence data by randomly sampling from the available area in equal number to the respective species presence data [22, 64]. Nonetheless, larger numbers tend to improve the predictive accuracy of models [67, 69].

The data analysed in this thesis has been recorded by GPS transmitters with good spatial and temporal resolution; the mean number of geo-referenced locations available per bird per month was 985.53. However, it has also been shown that it is important to have adequate spatial coverage for any spatial analysis [22] which in this case includes both the presences and the absences. As such, the approach taken here (and implemented in **Chapters 4** and **5**) was to generate five times more pseudo-absence locations than observed bird locations from an "available area". The available area was defined as the minimum bounding rectangle within which the locations for a given vulture occurred, in a given month (i.e., different available areas are applicable to each "bird-month"). This approach was deemed to provide adequate spatial coverage while also balancing the computational cost of each model fitted.

3 Daily properties in animal movement - quantifying temporal shifts

In this chapter, movement is centred on the daily activities of the target species. Four metrics of daily properties are described for each vulture: daily distance travelled, daily maximum displacement, daily overall displacement, and straightness of a daily path. An assessment is made to the patterns those metrics display over time, extending what has been presented so far in the literature. Patterns from individual vultures are contrasted to demonstrate the biological relevance of some of the findings. The *travellers* and *locals* are introduced.

Note: It is foreseen the publication the description of properties of daily movement in an African scientific journal to ensure the information reaches local stockholders working on the ground with vulture species.

3.1 Introduction

The movement capacity of an individual can be seen as its tendency to move according to both internal and external factors [1]. External factors include habitat structure and locations of key resources. The need to obtain food and other essential resources drives various ranging movements also termed "foraging" [4].

The foraging movements of large territorial vertebrates vary with age class, as differences in breeding status also lead to differences in the ways each exploits food resources [10, 70]. Pre-adult (non-breeding) individuals during dispersal periods typically target their movements at finding food resources [71]. Such individuals are non-territorial and search for patches with higher food availability. In turn, adult individuals settle and occupy breeding territories, and exhibit central-place foraging behaviour with movements centred around the nest [10]. Movements now also account for habitat choices, functional responses and a trade-off between foraging and safety. Breeding individuals seek a cost-benefit equilibrium in their foraging which considers the distance they need to cover and the benefits they can obtain (i.e., the food resources) [10]. The search for this balance is more acute in avian scavengers which depend on food resources that are both spatially and temporally unpredictable [12]. It may take days before they find food again the so the need to optimize their energetic gain at each feeding event at carcasses is higher [72].

Long-range movements in particular, may be infrequent but nonetheless play an important ecological role. Such movements may act as significant drivers of metapopulation dynamics, colonization, population spread, and biological invasions [73, 74]. “Long-range forays” are a particular type of long-range movement. They are long movements in spatial terms but relatively short in time, loops in which the animal departs from a regular foraging area, travels to remote locations, and returns to the initial area [73]. Moreover, long-range forays may reflect an adaptive exploratory foraging strategy to exploit remote food patches as well as other resources, and do not tend to be synchronised between conspecifics [73]. Describing differences in search efficiency among species is important to understand the mechanisms underlying species coexistence and so it is of major interest in the field of community ecology [75, 76]. The search performance, along with the general movement of an individual, is controlled by its motion and navigation (sensory and cognitive) aptitudes as well as its behaviour [1, 77]. The comparison between closely related species that exploit similar movement, cues and resources can help to understand the factors determining search efficiency [76].

Individual behavioural types, or “personalities”, such as activity, boldness and exploratory behaviour can shape the animal movement [70]. More aggressive species or individuals, for example, displace others in order to acquire larger territories [78]. Personality influences the way an individual perceives the environment and how it collects spatial information to build what it is called its “cognitive map” [79]. Nonetheless, it may be challenging to tease apart behavioural differences from the environmental heterogeneity, in explaining why movement varies among conspecifics [80]. The ways in which consistent intraspecific variation can affect movement have been studied mainly in the context of dispersal but also on foraging tactic. “Dispersal” relates to movements between habitat patches and breeding sites and are considered to be different from movements within patches or foraging areas [80]. Dispersal is a clearly delineated event in some species but not in others as a consequence of the continuous range of movement behaviours, and there is still no consensus in its definition [80]. Differences in morphology and behaviour have been linked and shown to have implications on niche partitioning, competition, or population dynamics (see [70] for a thorough review). Despite the close link between behaviour and movement, only recently these disciplines were inserted in a common theoretical framework for personality-dependent spatial ecology [70].

Although the coarser resolution from older technologies only allowed for a general description of space-use, it is possible nowadays to inspect in more detail the movement processes and individual decision making [70]. Movement descriptors include indices of distance or speed, the shape of a path

and the linkages of these indices across time and space. Distance indices include step size (e.g., distance between locations during a set time interval) and displacement (between consecutive locations, mean or maximum straight line distance covered during a set time interval). Shape indices include the straightness and tortuosity of a path [70].

The good spatial accuracy and temporal resolution of the satellite transmitters deployed in this study allow for an analysis of daily metrics. Such metrics can improve the understanding of movement patterns, foraging behaviour, and individual strategies taken. As such, this chapter focused on movement patterns of vultures at a daily scale. The aims were to:

i) describe four properties of daily movement based on distances travelled and the straightness of those paths: daily distance travelled, daily maximum and overall displacements, and straightness of a daily path;

ii) assess the temporal changes in those daily movement properties, for each vulture;

iii) examine the biological importance of the movement properties, both when considered individually and combined.

In particular, this chapter investigated the biological relevance of combined metrics to answer questions about whether vultures return to locations nearby their roost. It also investigated if the daily metrics could tease apart groups of vultures with distinct movement strategies.

3.2 Methods

3.2.1 Data specification

Prior to any assessment of the data, some pre-processing of the data was done and each day of tag deployment was excluded. Although there was no obvious change in behaviour on the day of deployment, the observations were excluded as a conservative measure. Those days with less than three vulture locations per bird were also excluded. Some tags were able to transmit bursts of locations so any locations recorded within a five-minute interval were reduced to one location to reduce the computational burden of analysis. After this reduction, the number of daily locations transmitted by the Savannah tags was still two to four times smaller than the alternative devices.

However, this was considered an acceptable balance between not excluding too many valuable data points, and potential effects on the comparison of resulting distances. In any case, animals were also analysed separately and so information provided by each tag was able to be compared with itself over time

After the initial data preparation, 225,820 locations from 17 vultures, transmitted between February 2015 and September 2018 were analysed. The monitoring period ranged from 74 days (2.4 months; tag ID 5215) to 1,150 days (more than three years; tag ID st2010-1332; **Table 3-1**). Fifteen birds were white-backed vultures (12 adults, one sub-adult, two immatures), two were hooded vultures (one adult and one immature). The sub-adult white-backed vulture (tag ID st2010-2700) was recorded as an immature following the SAFRING protocol but it was already carrying a metal ring when it was (re)captured so, it was subsequently coded as a sub-adult.

The geographic coordinates of the vulture locations were reported in degrees of latitude and longitude. These were projected to the Universal Transverse Mercator (UTM) system to convert the coordinate units to meters. UTM zone 33 South was used as it best represents the study region.

Table 3-1 Details of the 17 vultures studied between 2015 and 2018 in and around Namibia. The transmitter identification (Tag ID) is shown as well as the deployment date, as well as the start and end date of recorded locations included in the analysis, number of days monitored, deployment area (NP = National Park), species and age class. Tag ID for white-backed vultures shown in black and for hooded vultures highlighted in blue; sub-adult and immature highlighted in bold.

Tag ID	Deployment date	Start analysis	End analysis	Days monitored	Months monitored	Deployment area	Species	Age class
5215	2017-11-16	2017-11-17	2018-01-30	74	2.4	Etosha NP	White-backed vulture	Adult
5403	2017-04-11	2017-04-12	2018-06-12	426	14.0	Etosha NP	White-backed vulture	Adult
5404	2017-03-22	2017-03-23	2018-09-10	536	17.6	Kunene Region	White-backed vulture	Adult
5784	2017-07-18	2017-07-19	2018-03-30	254	8.4	Etosha NP	White-backed vulture	Adult
5785	2017-07-18	2017-07-19	2018-09-02	410	13.5	Etosha NP	White-backed vulture	**Immature**
5786	2017-08-19	2017-08-20	2018-09-10	386	13.7	Etosha NP	White-backed vulture	Adult
5787	2017-10-23	2017-10-24	2018-09-10	321	10.6	Bwabwata NP	White-backed vulture	Adult
5788	2017-11-02	2017-11-03	2018-09-10	311	10.2	Etosha NP	White-backed vulture	Adult
5789	2017-10-24	2017-10-25	2018-03-16	142	4.6	Bwabwata NP	White-backed vulture	Adult
CAT1	2017-10-24	2017-10-25	2018-09-05	315	10.4	Bwabwata NP	Hooded vulture	**Immature**
st2010-1330	2015-02-12	2015-02-13	2016-04-11	423	14.0	Bwabwata NP	Hooded vulture	Adult
st2010-1332	2015-02-16	2015-02-17	2018-04-10	1148	37.8	Bwabwata NP	White-backed vulture	Adult
st2010-2607	2017-02-15	2017-02-22	2018-09-04	559	18.4	Etosha NP	White-backed vulture	Adult
st2010-2608	2017-03-11	2017-03-12	2018-08-02	508	16.7	Etosha NP	White-backed vulture	Adult
st2010-2609	2017-05-26	2017-05-27	2018-04-26	334	11.0	Etosha NP	White-backed vulture	Adult
st2010-2697	2017-04-22	2017-04-23	2018-07-26	459	15.1	Etosha NP	White-backed vulture	**Immature**
st2010-2700	2017-05-28	2017-05-29	2018-09-05	464	15.2	Etosha NP	White-backed vulture	**Sub-adult**

Even though the vultures were tagged in Namibia, vultures also utilised its five neighbouring countries (Angola, Zambia, Zimbabwe, Botswana and South Africa; **Figure 3-1**). Eight vultures stayed within the regions where they were first located, the remaining nine travelled beyond that. The (two) hooded

vultures showed a much smaller geographic range than the (seventeen) white-backed vultures despite the variability between all birds (see also **Figure II. 1** to **Figure II. 17** in the Appendix for details).

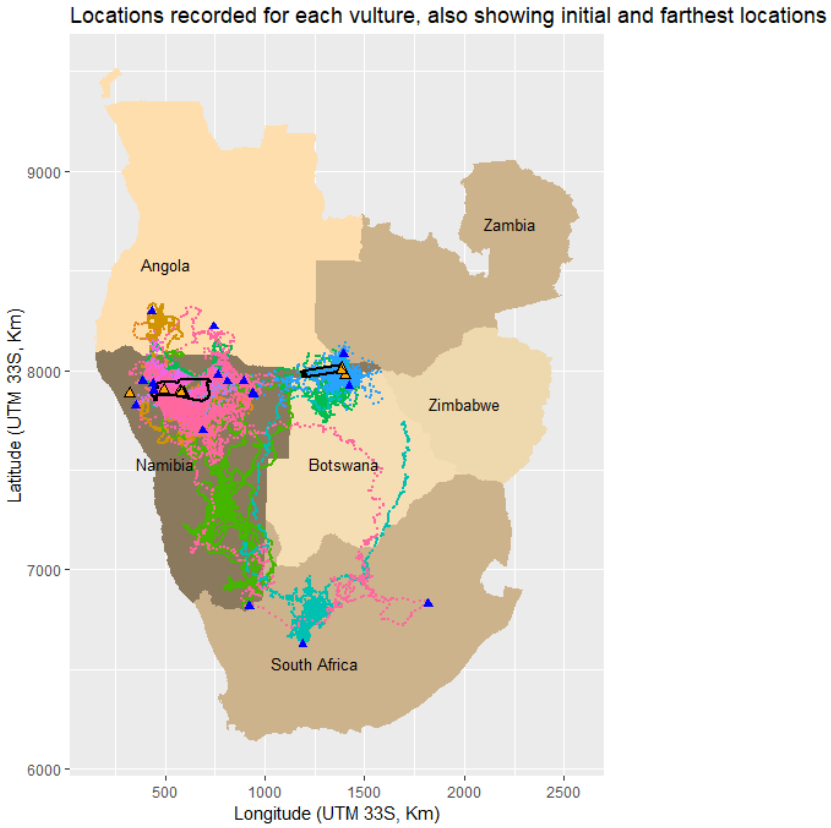


Figure 3-1 Locations shown for all individuals (coloured by individual) and its respective initial (orange triangles) and farthest (blue triangles) locations. The borders of Etosha National Park (NP; NW of Namibia) and Bwabwata NP (NE of Namibia) are also shown for reference.

The distances between the deployment location and the farthest location ever transmitted for each bird respectively were calculated (**Table 3-2**). The immature hooded vulture reached 84.40 km away from its first location after 191 days (6.3 months, bird with tag ID CAT1), the adult hooded vulture reached 98.88 km away after 211 days (almost 7 months, bird with tag ID st2010-1330). The father distance a white-backed vulture reached away from its initial locations ranged from 141.74 km (recorded by the immature individual with tag ID 5785 in 204 days) to 1,627.84 km (recorded by the sub-adult with tag ID st2010-2700 in 188 days). Two other birds flew farther than 1,000 km away from where they were first seen (tag IDs 5786 and 5789). The variability in geographic range of the vulture can be seen in **Figure 3-1**.

Table 3-2 Description of the farthest distances recorded from the deployment location for each. Tag ID is shown as well as the deployment date, data when farthest location was recorded, respective distance (km) and number of days it took the vulture to reach it. The total number of monitoring days and an index (km/day) to the farthest location are also shown. Tag ID for white-backed vultures shown in black and for hooded vultures highlighted in blue; sub-adult and immature highlighted in bold.

Tag ID	Deployment date	Farther distance date	Distance (km)	no. days to farthest	no. days monitored	Index to farthest (km/day)	Species	Age class
5215	2017-11-16	2017-12-15	446.36	29	74	6.032	White-backed vulture	Adult
5403	2017-04-11	2017-06-17	444.37	66	426	1.043	White-backed vulture	Adult
5404	2017-03-22	2018-07-31	493.48	496	536	0.921	White-backed vulture	Adult
5784	2017-07-18	2017-11-26	148.74	129	254	0.586	White-backed vulture	Adult
5785	2017-07-18	2018-02-09	141.74	204	410	0.346	White-backed vulture	**Immature**
5786	2017-07-19	2018-01-13	1,127.71	177	386	2.922	White-backed vulture	Adult
5787	2017-10-23	2018-08-28	997.25	309	321	3.107	White-backed vulture	Adult
5788	2017-11-02	2018-08-09	203.39	280	311	0.654	White-backed vulture	Adult
5789	2017-10-24	2018-02-06	1,385.03	104	142	9.754	White-backed vulture	Adult
CAT1	2017-10-24	2018-05-03	84.40	191	315	0.268	**Hooded vulture**	**Immature**
st2010-1330	2015-02-12	2015-09-10	98.88	211	423	0.234	**Hooded vulture**	Adult
st2010-1332	2015-02-16	2015-10-16	472.88	243	1148	0.412	White-backed vulture	Adult
st2010-2607	2017-02-15	2017-05-15	316.10	91	559	0.565	White-backed vulture	Adult
st2010-2608	2017-03-11	2017-12-13	241.63	275	508	0.476	White-backed vulture	Adult
st2010-2609	2017-05-26	2017-10-09	363.68	134	334	1.089	White-backed vulture	Adult
st2010-2697	2017-04-22	2018-03-24	230.37	336	459	0.502	White-backed vulture	**Immature**
st2010-2700	2017-05-28	2017-12-04	1,627.84	188	464	3.508	White-backed vulture	**Sub-adult**

To allow for the variable tag deployment lengths, an index was created to put the distance travelled into context. For each vulture, the distance travelled to the farthest locations was weighted by the total number of deployment days (**Table 3-2**, **Figure 3-2**). According to this index, there was a clear division between vultures (**Figure 3-2**). The four vultures that travel the furthest also show high indices; these were three adult white-backed vultures (tag IDs 5787, 5786 and 5789) and the sub-adult tag ID st2010-2700. Interestingly, one other adult white-backed that did not travel as far also shows a high index (tag ID 5215, travelled 446.36 km away from its initial location in a total of 74 days monitored).

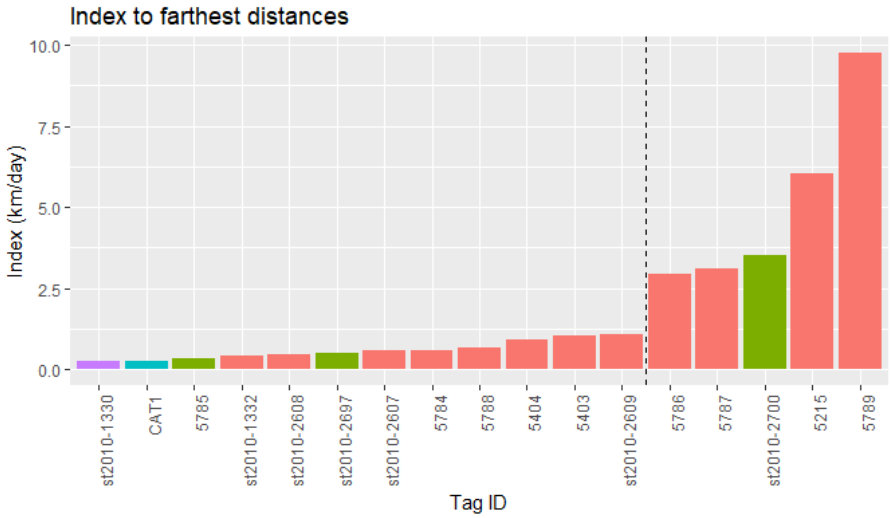


Figure 3-2 Illustration of the index to farther distances per vulture. Tag IDs are ordered per magnitude of the index, vertical dashed line highlights a possible separation between vultures. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; adult hooded vulture in purple, immature hooded blue.

3.2.2 Daily movement properties

Definitions and initial data inspection

Four characteristics were calculated to examine daily movement patterns, as per Spiegel *et al.* [76]. Distances were, strictly speaking, minimum distances as they depend on the temporal resolution of the data; also, days were defined as the twenty-four-hour period, from one midnight to the next.

The daily distance travelled (DDT) was calculated by summing the straight-line distances between all consecutive locations in a day (**Figure 3-3**). The daily overall displacement (DOD) was calculated as the straight-line distance from the first to the last location of the day. The daily maximum displacement (DMD) was calculated as the straight-line distance from the first to the farthest location of the day. The straightness of a daily path (SDP) was calculated as the ratio between the DMD and the sum of the straight-line distances between successive locations from the first to the farthest location in a day.

While three of the four measures returned a distance as a metric, SDP is a ratio where the numerator (DMD) is always smaller than the denominator and thus could only vary between zero and one. This ratio close to zero represent erratic flights approached one for perfectly straight flight. The distance between locations were calculated using the sp package [81] in R [62].

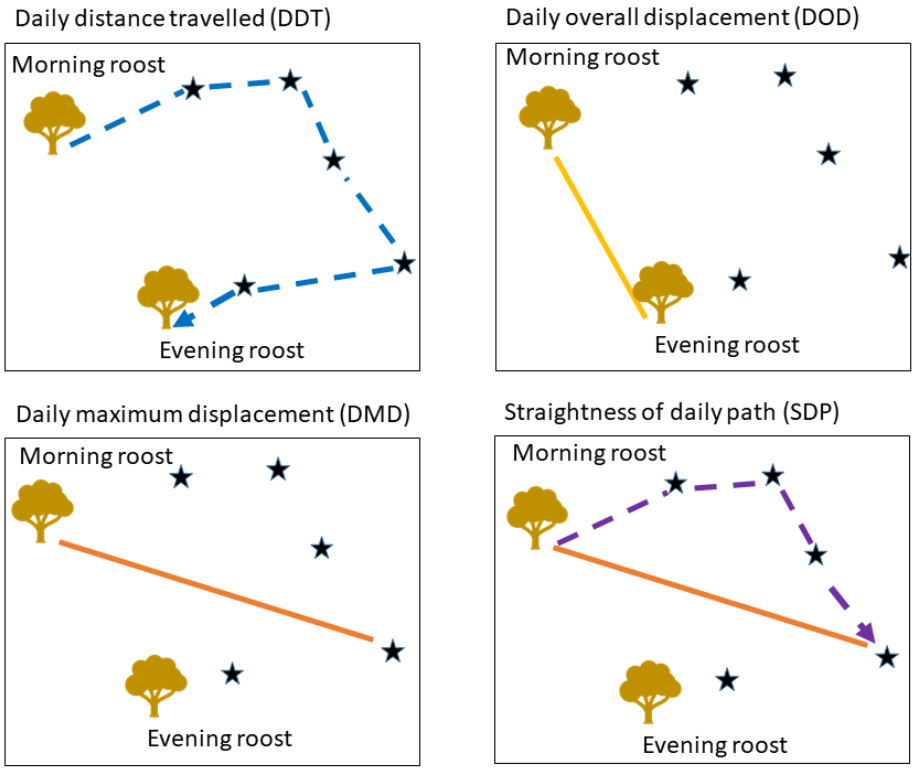


Figure 3-3 Diagram showing the four properties calculated to examine the daily movement patterns. Trees represent the start and end point each day (morning and evening roost), stars represent the GPS locations received, arrows point to a sequence of movement (distances measured), and straight lines show displacements.

The properties from 6,604 days of the 17 vultures were analysed. Metrics were summarised per species and showed clearly distinct daily properties (**Table 3-3**). Caution should to be made though as there are only two hooded vultures and the number of days analysed per species also varied considerably. Overall, the white-backed vultures showed higher daily properties than the hooded vultures.

Table 3-3 Summary of the properties of daily movement patterns per species. Details for each individual vulture are illustrated in the figure below and shown in the **Appendix III**. Mean, 95% confidence intervals (inside square brackets) and range (inside round brackets) are show. Distances as follow: daily distance travelled (DDT), daily overall displacement (DOD), daily maximum displacement (DMD), straightness of a daily path (SDP). The total number of days analysed per species is also shown (sum of the respective *n* individuals).

Species	Number of days	DDT (km)	DOD (km)	DMD (km)	SDP
White-backed vultures (n=15)	5864	94.09 [0.42;256.83] (0.01-429.17)	39.86 [0.01;157.42] (0.000-357.65)	48.77 [0.12;158.63] (0.005-358.52)	0.70 [0.27;0.99] (0.06-1.00)
Hooded vultures (n=2)	740	46.44 [0.51;153.93] (0.22-229.78)	13.95 [0.01;66.02] (0.002-108.06)	20.38 [0.14;69.89] (0.02-108.45)	0.68 [0.21;0.99] (0.05-1.00)

Individually, each bird showed a large variation in the daily properties (**Figure 3-4** and **Table III. 1** in the Appendix). There was a visible fluctuation around the overall mean (shown in the dashed horizontal lines in each plot); the range of the inter-quantile value varies slightly between birds, although some birds share overlapping range values. While visual inspection of these metrics is useful, it is also useful to discern if there is evidence for any systematic patterns across individuals and time – time considered using months and/or season.

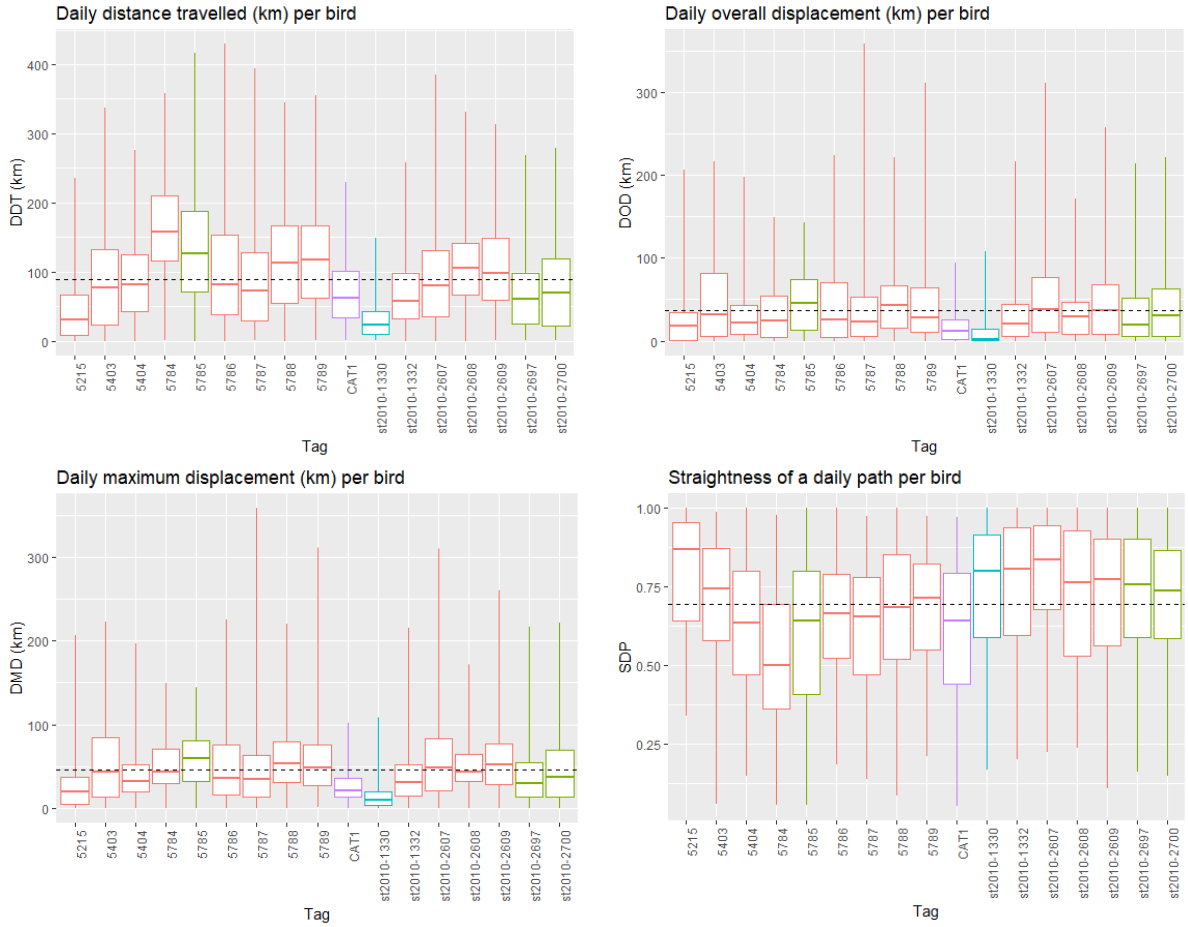


Figure 3-4 Variation in the properties of daily movement patterns per individual. Box plots show the 25% (bottom), 50% (middle) and 75% (top) quantiles, as well as the minimum (extent of the lower line) and maximum (extent of the upper line) values. Colours represent species and age classes: light red – adult white-backed, green – sub-adult and immature white-backed, blue – adult hooded, purple – immature hooded. The horizontal dashed line in each of the plots shows the overall mean for the metric, for reference.

Model structure

Any variation in the daily movement properties across individuals through time was formally assessed at different temporal scales; month, season and by pooling data across the entire deployment period. The mean variation of the daily metrics was modelled using a Generalised Linear Model (GLMs, [53]) as a function of vulture ID and time (month and season). Each time frame was considered unique, i.e., January 2017 was treated separately from January 2018, and the same for the seasons; year-month and year-season combinations were used, respectively.

GLMs are extensions of linear models that allow for non-linearity (restricted to monotonic shapes) and non-constant variance patterns in the data, given the model [54]. GLMs are based on a relationship between the mean of the response variable and the linear combination of the explanatory variables; and the linearity is not with the raw response but is achieved via a link function. Also, the data may be assumed to be from several families of probability distributions, including the Gamma or Beta distribution.

Five candidate models were tested, for each daily movement property:

1. a model containing only tag ID, herein referred to as *model T*:

$$g(E[Y_i]) = \beta_0 + \boldsymbol{\beta}_{tag.ID} \ ;$$

2. a model containing tag ID and each year-month combination, herein referred to as *model TYM*:

$$g(E[Y_i]) = \beta_0 + \boldsymbol{\beta}_{tag.ID} + \boldsymbol{\beta}_{year.month} + \boldsymbol{\beta}_{tag.ID:\, year.month} \ ;$$

3. a model containing tag ID and each year-season combination, herein referred to as *model TYS*:

$$g(E[Y_i]) = \beta_0 + \boldsymbol{\beta}_{tag.ID} + \boldsymbol{\beta}_{year.season} + \boldsymbol{\beta}_{tag.ID:\, year.season} \ ;$$

4. a model containing each year-month combination, herein referred to as *model YM*:

$$g(E[Y_i]) = \beta_0 + \boldsymbol{\beta}_{year.month} \ ;$$

5. a model containing each year-season combination, herein referred to as *model YS*:

$$g(E[Y_i]) = \beta_0 + \boldsymbol{\beta}_{year.season} \ .$$

where Y_i is each response variable (DDT, DOD, DMD or SDP) at time i. β_0 represents the intercept, $\boldsymbol{\beta}_{tag.ID}$ represents the vector of coefficients for tag ID (one for bird, up to 16), $\boldsymbol{\beta}_{year.month}$ represents

the vector of coefficients for year-month (one for each combination, up to 43), $\boldsymbol{\beta}_{year.season}$, represents the vector of coefficients for year-season (one for each combination, up to 11). $\boldsymbol{\beta}_{tag.ID:\,year.month}$ represents the interaction of tag ID with year-month, which allows a different set of coefficients for each bird in each of its year-month combinations (up to 247), $\boldsymbol{\beta}_{tag.ID:\,year.season}$ represents the interaction of tag ID with year-season, allowing a different set of coefficients for each bird in each of its year-seasons combinations (up to 77).

The linear expression is achieved by a link function $g(\cdot)$, here the log to ensure the outcome is also non-negative with $g(E[Y_i]\,) = \log(E[Y_i])$.

Furthermore, the distances calculated (i.e., DDT, DOD, DMD) are continuous positive measures and are described assuming the Gamma distribution where $Y \sim Gamma\,(k, \theta)$, where k is a shape parameter and θ is a scale parameter. Also, the mean variance relationship is known and can be expressed as $Var = \phi.\mu^2$, where ϕ is a dispersion parameter.

In turn, the straightness of daily paths (SDP) are continuous measures bounded by 0 and 1 and appropriately described by the Beta distribution with $Y \sim Beta(\alpha, \beta)$, where both α and β represent shape parameters. The mean variance relationship is also known and can be expressed as

$Var = {\mu(1-\mu)}/{1+\phi}$, where ϕ is a precision parameter.

Residual auto-correlation

Of note is the autocorrelation inherent in the animal locations over time (within individual) and to ensure model results were reliable, this feature was accounted for by permitting a residual correlation structure in each model. This consideration requires the longevity of any residual correlation within animals to be characterised and after investigation using autocorrelation function plots of model residual, blocks of "bird-week" were used in the calculation of robust standard errors for model-based parameter estimates.

Model selection and assessment

K-fold cross validation (CV) was used to choose between the models stated above. K-fold CV has computational costs and operates by partitioning the data set into K sub-sets of similar size (K is typically between 5 and 10; see [82] for a review). (K−1) folds are used to construct a model, while the sample left-out is used for validation. This operation iterates K times, with each of the K folds

successively being assigned as validation data. In this instance, 10-fold cross validation was used with 100 resamples (owing to the stochastic nature of the selection of folds). For information, Akaike (AIC, [83]) and Bayesian information criteria (BIC, [84]) are also presented in the results.

Model assessment was performed using visual and numerical diagnostics. Overall model suitability was visually assessed by plotting the observed against fitted values, with suitability characterised by no systematic patterns which deviate from the 45° line. The independence in model errors (by inspection of their estimates, residuals) was not assumed for these models and so was not inspected. However, the suitability of the time window which defined the correlation blocks (bird-week) was visually inspected using autocorrelation function (ACF) plots. In this case, correlation block suitability was evidenced by an ACF which decays to zero, on average, during the length of the proposed correlation block (e.g., one week of transmission for one bird). Lastly, the adequacy of the distribution selected for the response variable, given the model, was tested by contrasting the mean-variance relationship of the fitted values and model residuals, with that assumed under the model.

To appreciate the uncertainty about any model predictions based on the best candidate model, this uncertainty was based on the robust standard errors, via 500 parametric bootstraps from the model coefficients. The uncertainty around each expected mean properties was captured with the lower and upper 95% confidence limit, taken from the respective quantiles from the bootstraps.

All statistical procedures were implemented using R version 3.6.0 [62], with RStudio v. 1.1.456 [85]; Gamma models were fitted using the MRSea package v. 1.0.1 [61] whereas the Beta models were fitted also using the betareg package [86]. Plotting was done mostly with the ggplot2 package [87]; the basic visualization tools in R were also used.

3.3 Results

3.3.1 Daily distance travelled (DDT)

Model selection

Figure 3-5 shows the CV scores with 95% confidence intervals for each of the five models trialled. All models presented non-overlapping confidence intervals around the mean CV score. The *model TYM* was indicated as the best (i.e., lowest score) based on this criterion. Additionally, the AIC score was lowest for the *model TYM* and the BIC score was lowest for the *model T* (**Table III. 2** and **Figure III. 1** in the Appendix).

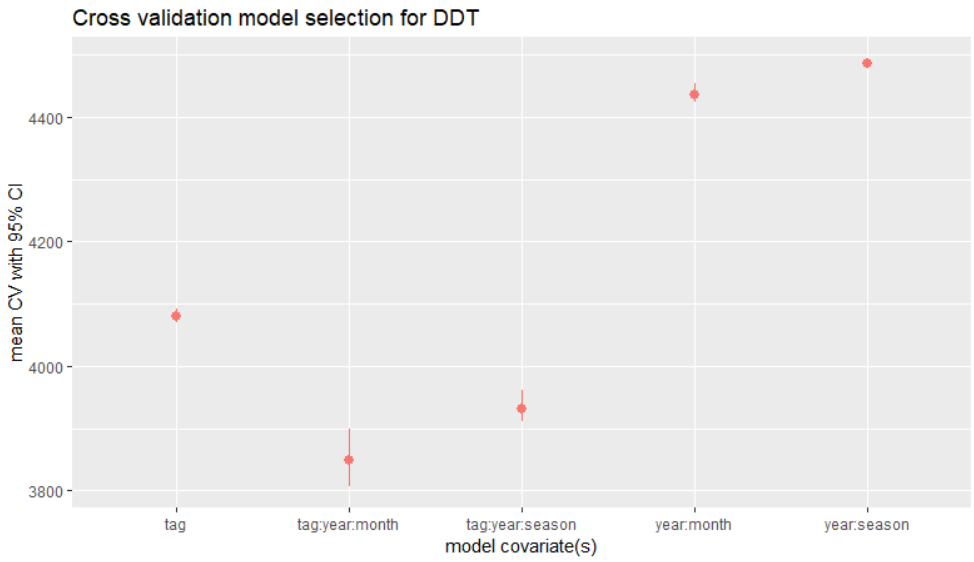


Figure 3-5 Performance of the models tested for daily distance travelled (DDT) resultant from 10-fold cross validation; mean CV score with 95% confidence intervals shown.

Best model assessment

The model selected showed some under- and over-predictions but seemed to describe well the mean DDT and there were no issues with model fit evidenced here (**Figure 3-6**).

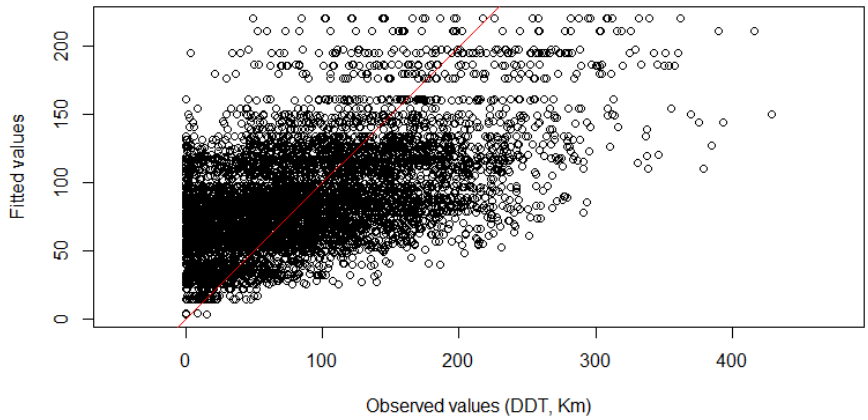


Figure 3-6 Observed measures of daily distance travelled (DDT) and fitted values from the selected model. Red line shown to aid interpretation (1,1).

Suitability of the correlated blocks used in the model was inspected with an autocorrelation function plot (**Figure 3-7**); it was visible that on average (red line) there is a decay to almost zero in the correlation of residuals during the correlated block duration, a bird-week. This block specification was deemed to be appropriate and used for the remainder of the movement properties (**Figure III. 3** in the Appendix).

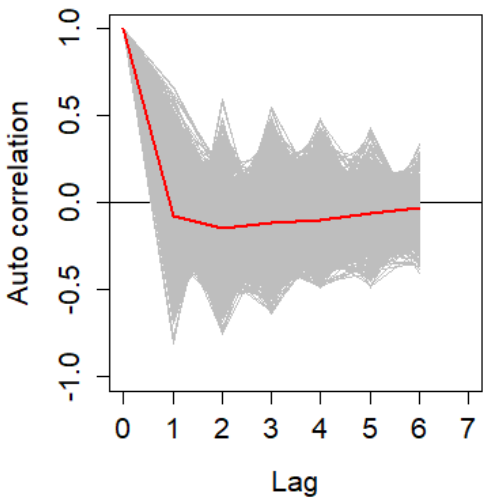


Figure 3-7 Visual assessment on the independence of model residuals. The autocorrelation function plot shows the decay inside each block in the grey lines, and the mean decay in the red line. Each lag represents a day.

The assumed mean-variance relationship (red dashed line) was slightly steeper than the observed mean-variance relationship (dots) (**Figure 3-8**). This indicated that larger estimated values of daily distance travelled will have their variance under estimated; confidence intervals for these values will be narrower than they should be.

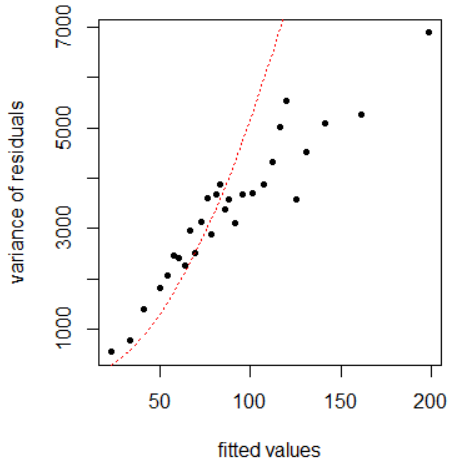


Figure 3-8 Visual assessment of the variance in the best candidate model residuals. The observed mean and variance of residuals is shown with the points, and the theoretical relationship is shown with the red line.

Model results

The predictions generated from the best candidate model (the *model TYM*) for each combination of tag ID, year and month showed significant variation in the mean daily distance travelled along time within individuals (**Figure 3-9**, and **Table III. 3** in the Appendix). Fluctuation was visible in all birds with each showing its own pattern. All but two white-backed vultures showed oscillations around the predicted overall DDT mean (i.e., the mean for all 17 birds combined, 88.75 km); birds with tag IDs 5784 and 5789 travelled above average distances routinely. The hooded vultures showed similar pattern as the white-backed vultures, but with lower values of DDT.

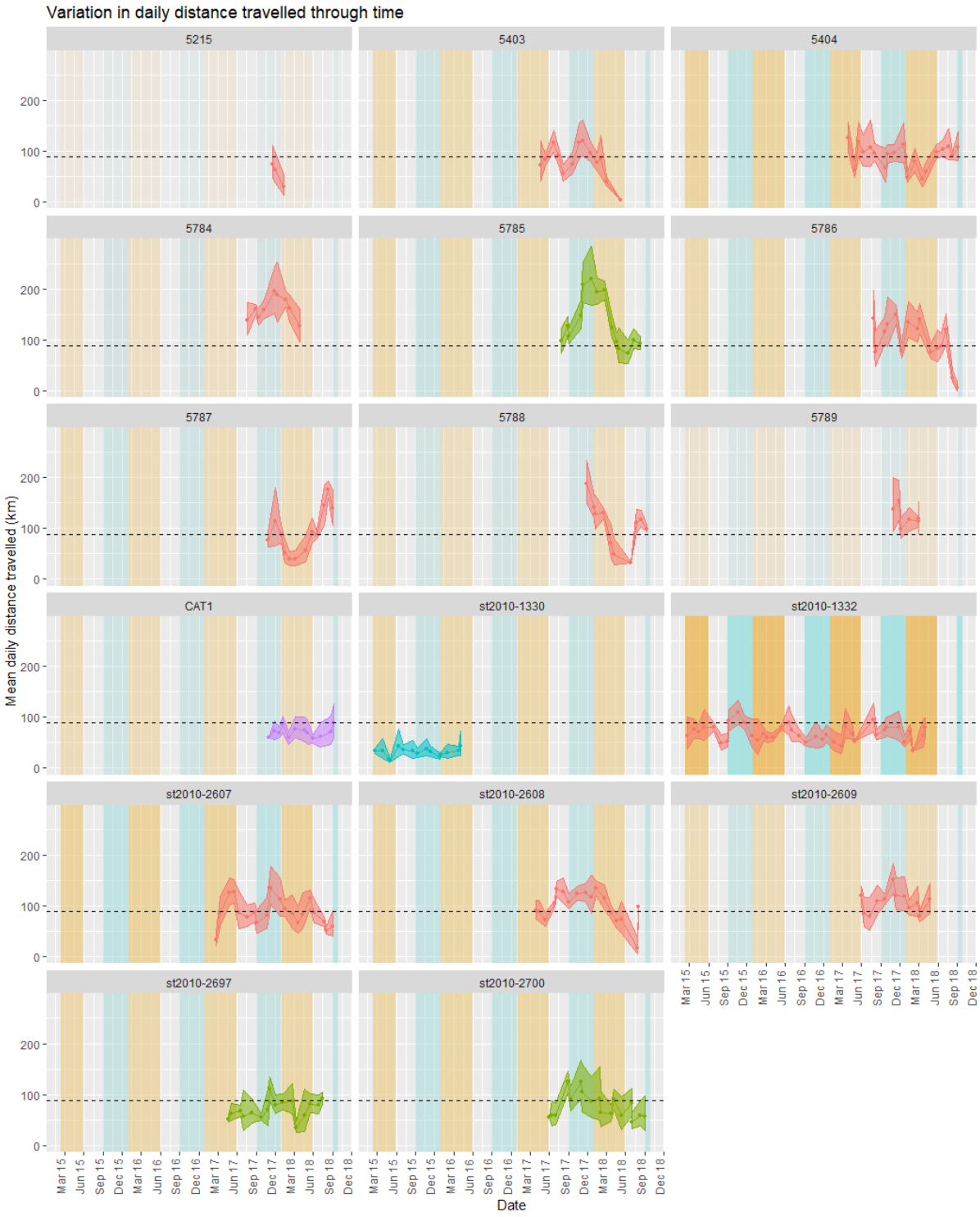


Figure 3-9 Variation in the daily distance travelled (DDT, km) for each individual generated by the best candidate model. Mean predictions with respective 95% CI bands are shown. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; immature hooded in purple; adult hooded in blue. Seasons along the year coloured differently: hot wet in golden, cold dry in grey, small rain in blue. Dashed horizontal line represents the overall DDT mean, for all 17 birds.

Figure 3-9 displays each mean estimate of the DDT per month with associated uncertainty, generated by the best candidate model. For each bird, the minimum and maximum of those monthly estimates were selected. The temporal variation of the minima and maxima mean DDT was noticeable. Broadly, birds seemed to reduce their mean daily distance travelled as the year was starting (**Figure 3-10**). Ten (58.82%) vultures had an expected lowest mean DDT between January and May (during the hot wet season); among these were one immature white-backed (tag ID st2010-2697), and both hooded vultures (tag IDs CAT1 and st2010-1330). As the year progressed minima DDT were still prevalent, and the remainder immature white-backed vultures had their minima DDT in June and July (tag IDs 5785 and st2010-2700, respectively). Later in the year the expected maxima DDT increased largely with 12 birds (70.59%) showing the highest mean DDT between September and December (during the small rainy season). Among these were two immature white-backed (tag IDs 5785 and st2010-2697) and the immature hooded vulture (tag ID CAT1). The third immature white-backed had its maxima in August (tag ID st2010-2700) and the adult hooded vulture in April (tag ID st2010-1330). Overall five birds (29.41%) had synchronous records of expected minima and maxima DDT within a season (**Table III. 3** in the Appendix).

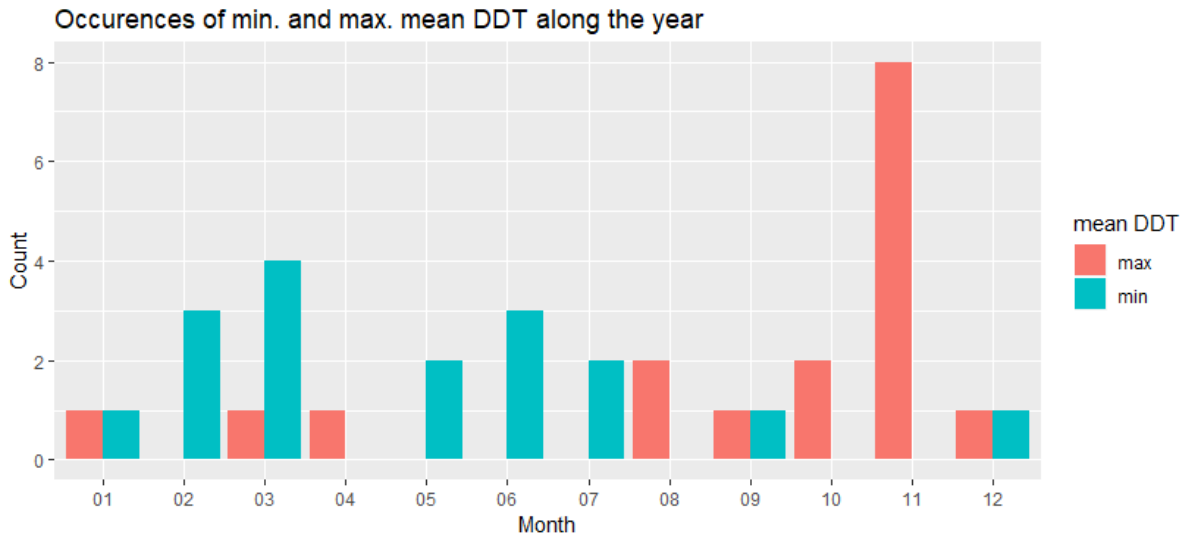


Figure 3-10 Occurrence of the minima (blue) and maxima (red) mean monthly daily distance travelled (DDT) predicted for each bird along the year. All birds are present, note each coloured count will sum to 17

3.3.2 Daily overall displacement (DOD)

Model selection

Three of the candidate models failed to converge (models *TYM*, *TYS*, and *YM*); different approaches were tested such as removing some outlying data points, but none proved useful. Therefore, those models were excluded from further consideration. The remaining two candidate models showed distinct CV scores with *model T* having the lowest CV score of the two (**Figure 3-11**). As such, *model T* was elected as the best candidate to describe the DOD. Interestingly, *model T* also showed lowest AIC and BIC scores (**Table III. 4** and **Figure III. 2** in the Appendix).

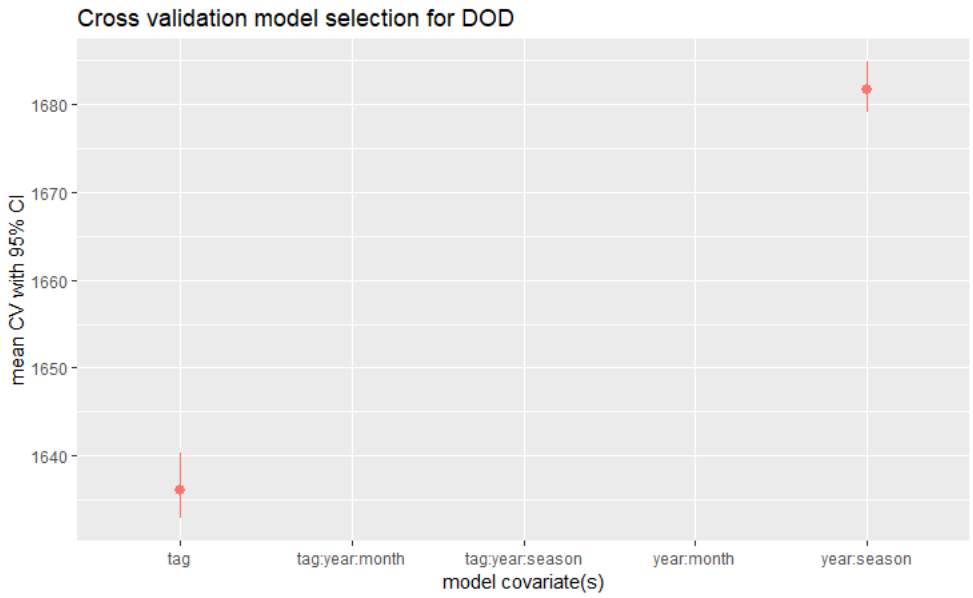


Figure 3-11 Performance of the models tested for daily overall displacement (DOD) resultant from 10-fold cross validation; mean CV score with 95% confidence intervals shown. Three of the models did not converge and as such no selection scores are available.

Best model assessment

The best model estimated values of DOD as high as 51.41 km, but not as high as the observed data (up to 357.65 km) (**Figure 3-12**). This was expected given that predictions based on these models are mean values for each tag and so would not normally capture the full range of the observed/input data in any case.

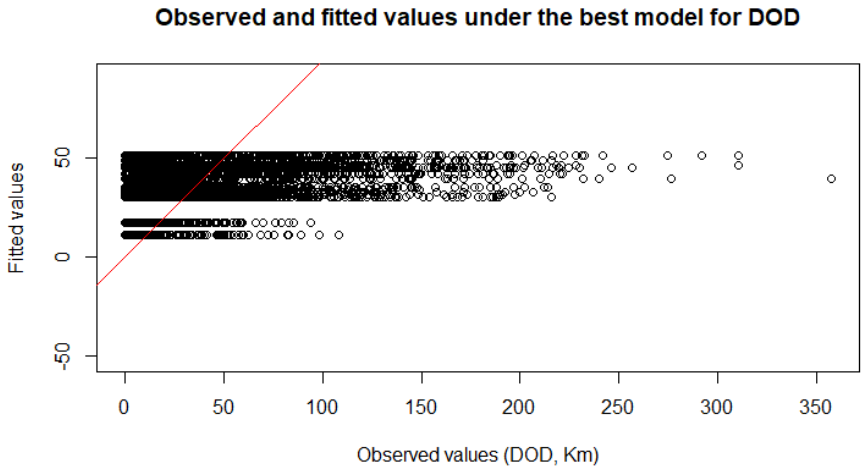


Figure 3-12 Observed measures of daily overall displacement (DOD) and fitted values from the selected model. Red line shown to aid interpretation (1,1).

The mean-variance relationship assumed under the model (red dashed line) appears to be a good approximation to the mean-variance relationship observed here (dots) (**Figure 3-13**).

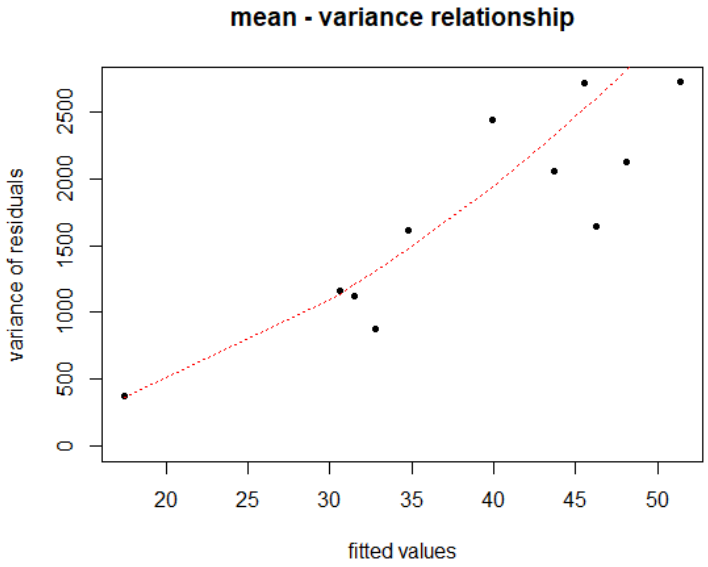


Figure 3-13 Visual assessment of the variance in the best candidate model residuals. The observed mean and variance of residuals is shown with the points, and the theoretical relationship is shown with the red line.

Model results

The predictions generated from the best candidate model (*model T*) for each tag, illustrate significant differences in the mean daily overall displacement between some individuals (**Figure 3-14** and **Table III. 5** in the Appendix). Two birds show a very wide confidence interval around the mean DOD (tag IDs 5215 and 5789) which included the overall mean DOD (36.96 km, for all 17 birds). Moreover, there was a statistical separation of two groups of birds, with non-overlapping 95% CI. The predicted values for one immature (tag ID 5785) and four adults white-backed vulture (tag IDs 5403, 5786, 5788, and st2010-2607) were always larger than the mean predictions for three other adults (tag IDs 5404, st2010-1332, and st2010-2608).

The estimates of DOD for the immature hooded vulture (tag ID CAT1) were significantly smaller than those of the white-backed; the predictions for the adult hooded vulture (tag ID st2010-1330) were even lower and thus, also non-overlapping with the other species.

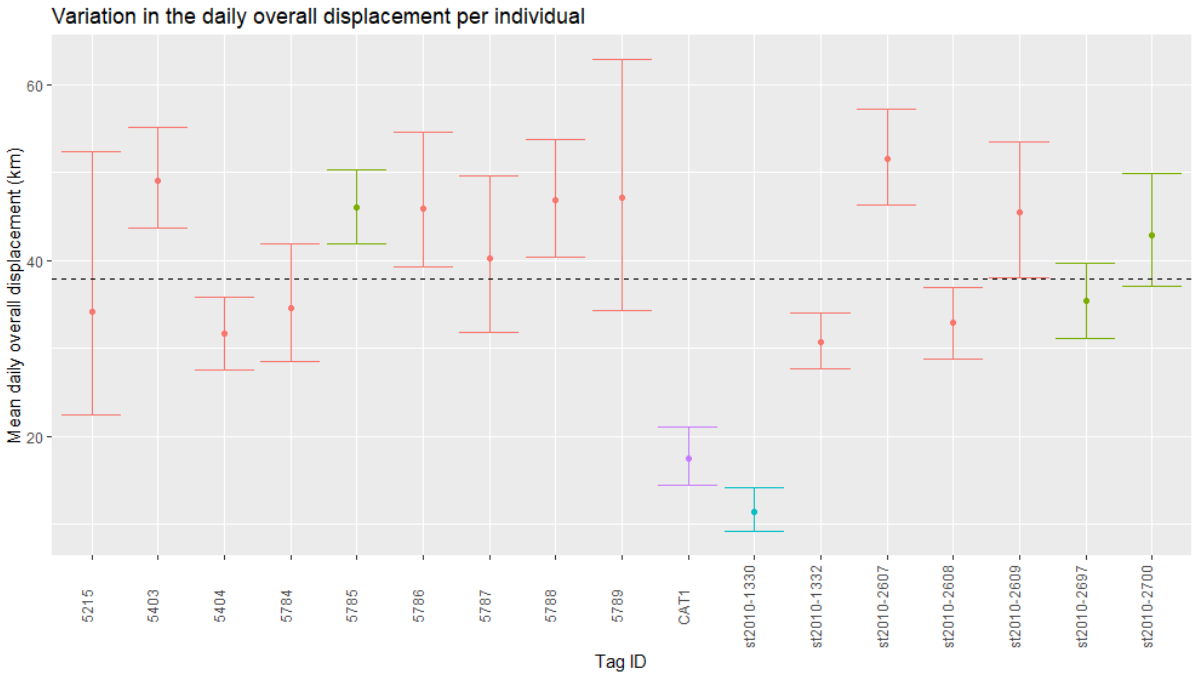


Figure 3-14 Variation in the daily overall displacement (DOD, km) for each individual generated by the best candidate model. Mean predictions with respective 95% confidence intervals are shown. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; immature hooded in purple; adult hooded in blue. Dashed horizontal line represents the overall DOT mean. Dashed vertical lines separate the years.

3.3.3 Daily maximum displacement (DMD)

Model selection

Two candidate models, *model TYS* and *model TYM* returned small CV scores with confidence intervals that overlapped (**Figure 3-15**). *Model TYS* had the lowest average CV score and so was selected as best candidate to describe the DMD. Interestingly, the AIC score was lowest for *model TYM* and the BIC score was lowest for a *model T* (**Table III. 6** and **Figure III. 4** in the Appendix).

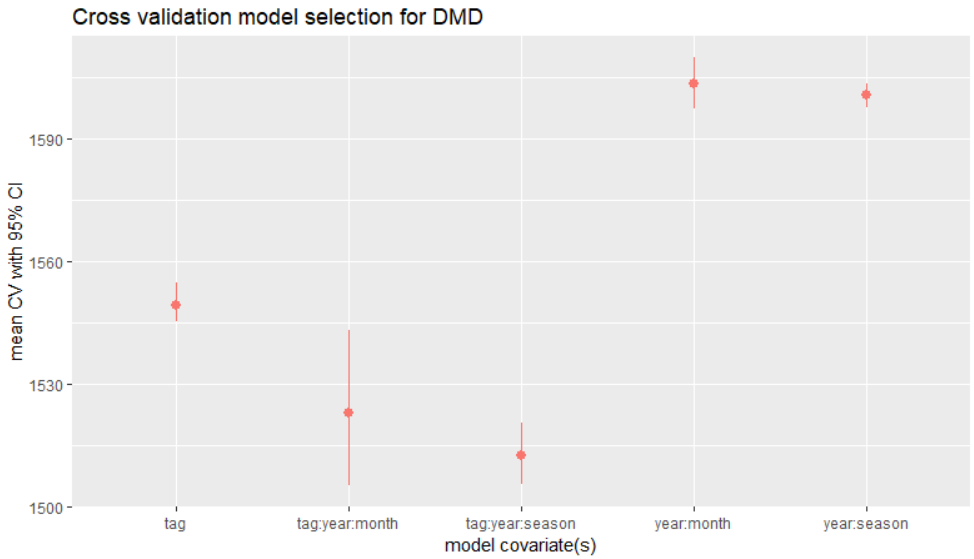


Figure 3-15 Performance of the models tested for daily maximum displacement (DMD) resultant from 10-fold cross validation; mean CV score with 95% confidence intervals shown.

Best model assessment

The selected model showed some under- and over-predictions. Values of DMD were estimated up to 86.98 km, not as high as the observed (up to 358.52 km), although that difference only captures small number of the records (13%; **Figure 3-16**). As before, this was unsurprising as the predictions based on these models relate to the mean.

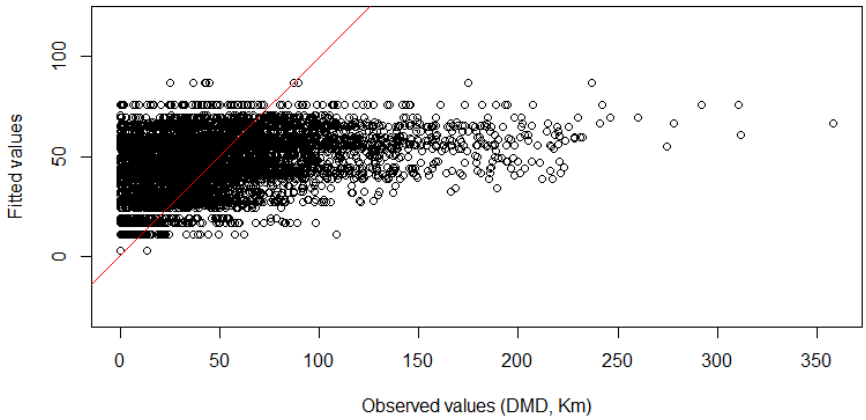


Figure 3-16 Observed measures of daily maximum displacement (DMD) and fitted values from the selected model. Red line shown to aid interpretation (1,1).

The model assumed for the mean-variance relationship (red dashed line) appears to be a very good fit to that observed (dots) (**Figure 3-17**).

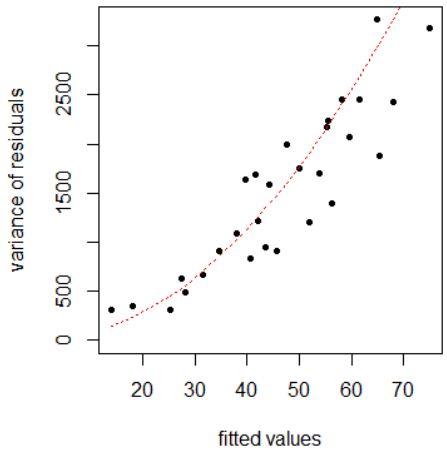


Figure 3-17 Visual assessment of the variance in the best candidate model residuals. The observed mean and variance of residuals is shown with the points, and the theoretical relationship is shown with the red line.

Model results

The predictions for DMD from the best candidate model (*model TYS*) for each combination of tag, year and season showed variations of the mean daily maximum displacement predicted through time within individuals (**Figure 3-18**, and **Table III. 7** in the Appendix). Fluctuation was visible between consecutive seasons with each bird showing slightly distinct patterns. The predictions for all vultures

included the overall DMD mean (45.59 km, for all 17 birds); the bird with tag ID st2010-1332 showed the most prominent oscillation as time went by. Both hooded vultures (tag IDs CTA1 and st2010-1330) showed little oscillation in DMD along seasons, with a slight increase as time progresses; the adult hooded vulture had the lowest expected DMD.

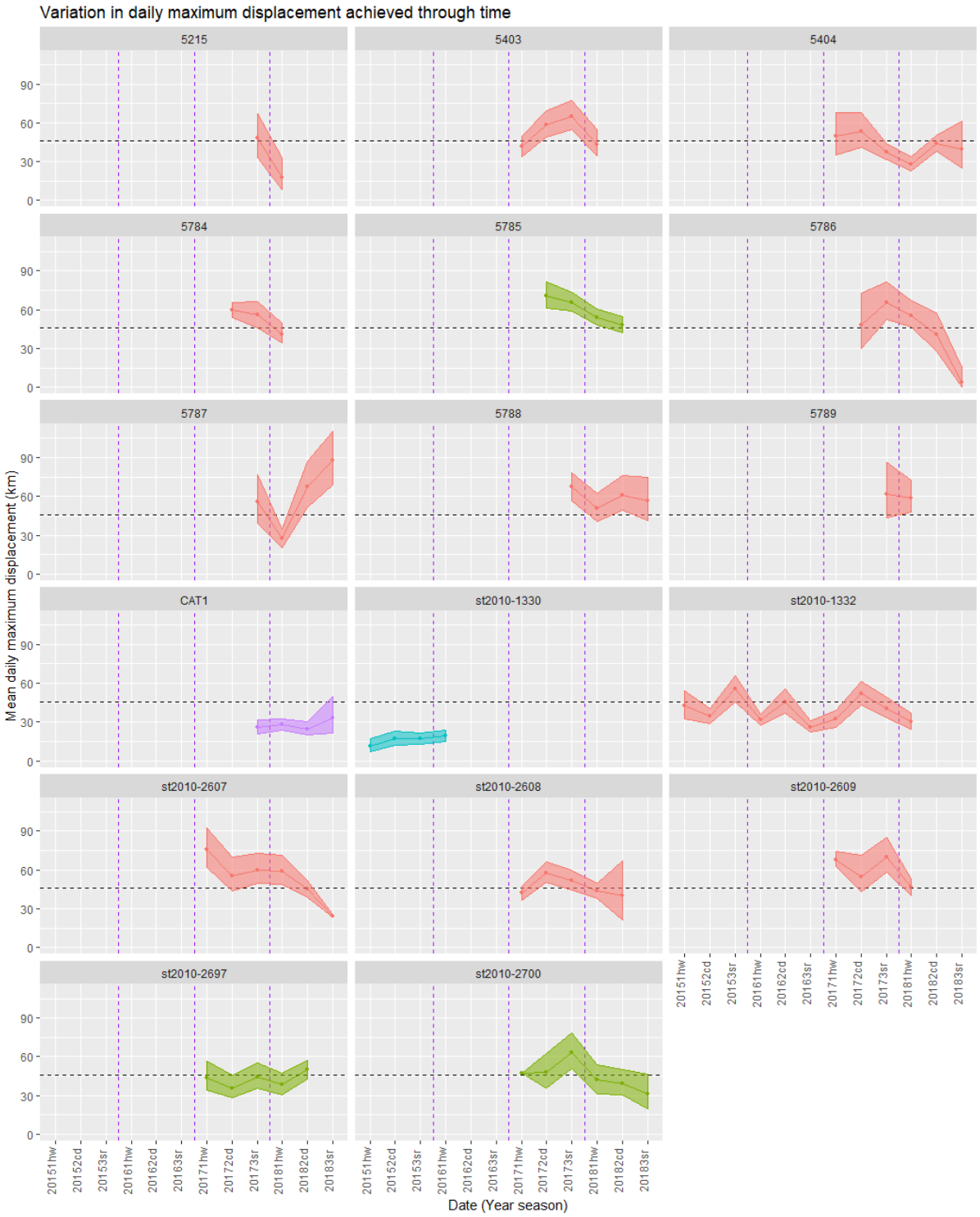


Figure 3-18 Variation in the daily maximum displacement (DMD, km) for each individual generated by the best candidate model. Mean predictions with respective 95% CI bands are shown. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; immature hooded in purple; adult hooded in blue. Seasons are indicated with the respective year and shortened in the x-axis (Date) as: 1hw- hot wet, 2cd- cold dry, 3sr- small rain. Dashed horizontal line represents the overall DMD mean. Dashed vertical lines separate the years.

Figure 3-18 displays each mean estimate of the DMD per season with associated uncertainty, generated by the best candidate model. For each bird, the minimum and maximum of those seasonal estimates were selected. The temporal variation of the minima and maxima seasonal mean daily maximum displacement was also perceptible. As the year begins, the number of expected minima peaks. Nine birds (52.94%) their lowest mean DMD during the hot wet season; these included eight adult white-backed and the adult hooded vulture (**Figure 3-19**). This latter also recorded its maxima mean DMD during the hot wet season. As the year progresses, the number of expected minima and maxima mean DMD was quite even, with four and five records respectively. Two immature white-backed vultures had both their expected minima and maxima during this season (tag IDs 5785 and st2010-2697), the immature hooded and one adult white-backed showed their minima during the cold dry months. Later in the year, the number of minima records stayed the same but on the other hand, the number of expected maxima mean DMD reached its highest. Ten birds (58.82%) have an expected maximum during the small rain season. These include eight adults and one immature white-backed vulture (tag ID st2010-2700, which also shows its minima record then) and the immature hooded vulture. Overall seven birds (41.18%) had synchronous records of expected minima and maxima DMD within a season (**Table III. 7** in the Appendix).

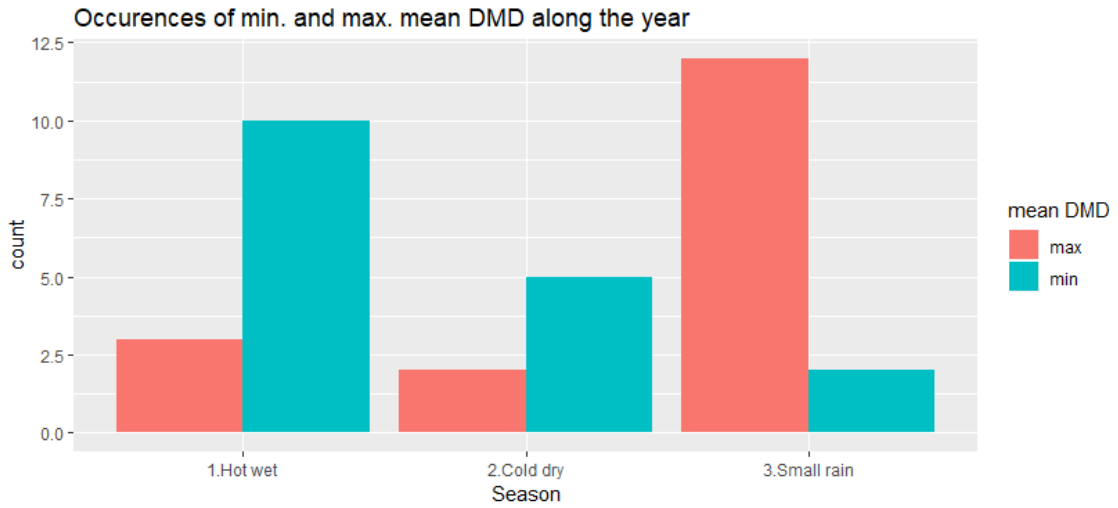


Figure 3-19 Summary of occurrence of the minimum (in blue) and maximum (in red) records of mean seasonal daily maximum displacement (DMD) predicted for each bird. Seasons: 1.Hot wet - January to May, 2.Cold dry - June to August, 3.Small rain – September to December.

3.3.4 Straightness of a daily path (SPD)

Model selection

The candidate models with the lowest mean CV score were *models T* and *TYS*, and their confidence intervals slightly overlapped (**Figure 3-20**). Additionally, the AIC and BIC scores were the lowest for *model T* (**Table III. 8** and **Figure III. 5** in the Appendix). The model selected as best candidate to describe patterns in the SDP was *model T*; nonetheless, given the negligible difference on the AIC score and the potential for relevant biological insights, *model TYS* was also considered.

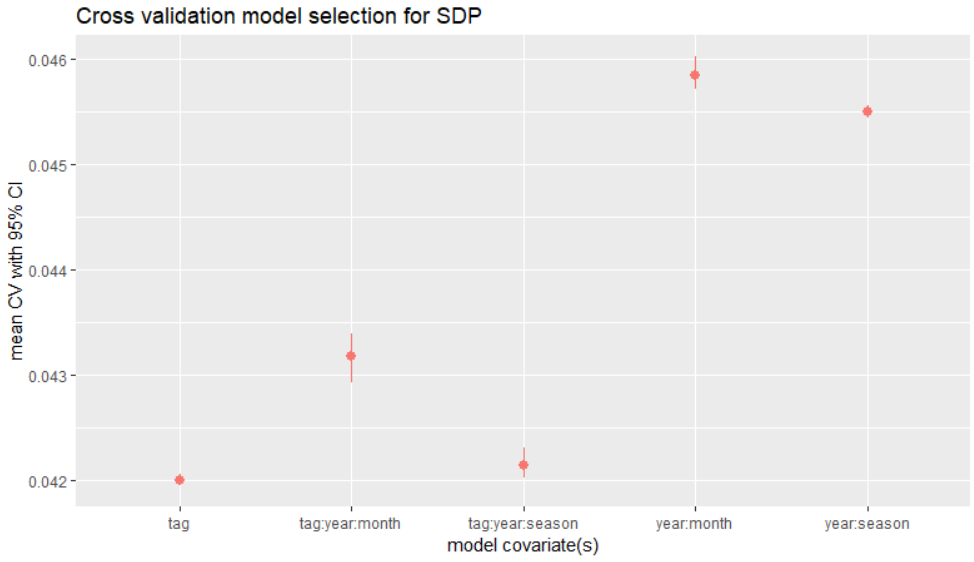


Figure 3-20 Performance of the models tested for straightness of a daily path (SDP) resultant from 10-fold cross validation; mean CV score with 95% confidence intervals shown.

Best model assessment

The selected model estimated SDP as low as 0.52, not as low as the observed (down to 0.05); that difference contained 21% of the records (**Figure 3-21**). Nonetheless, this pattern was of no concern as the predictions based on these models do not normally capture the full range of the observed values.

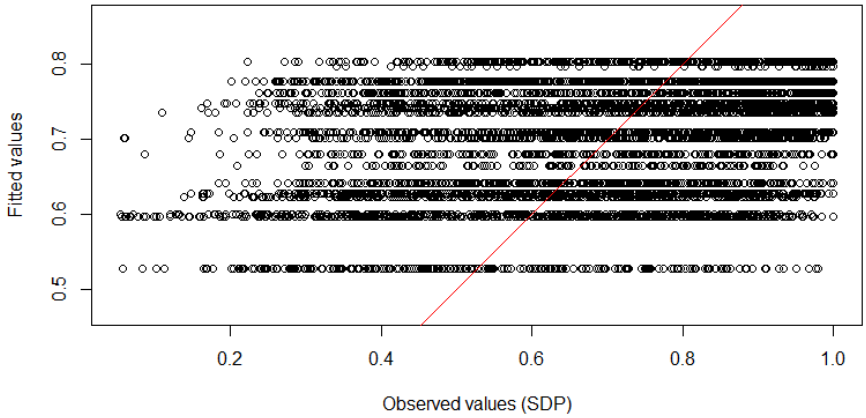


Figure 3-21 Observed measures of straightness of daily path (SDP) and fitted values from the selected model. Red line shown to aid interpretation (1,1).

Overall, the model residuals seemed to follow the pattern expected for the theoretical mean-variance relationship under a Beta distribution (**Figure 3-22**, left hand side); in more detail, there seemed to be slight deviations from the expected residual variance, with some over and some under estimation of the variance (**Figure 3-22**, right hand side).

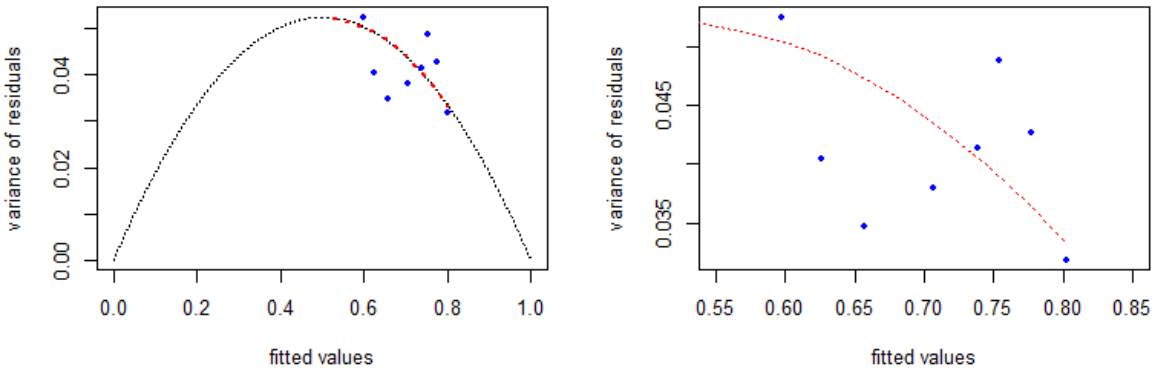


Figure 3-22 Visual assessment of the variance in the best candidate model residuals. The observed mean and variance of residuals is shown with the points, and the theoretical relationship is shown with the red line (full range of SPD on the left hand side, detailed section on the right hand side).

Model results

The predictions generated from the best candidate model (*model T*) illustrated significant differences in the mean straightness of a daily path (SDP) between individuals (**Figure 3-23** and **Table III. 9** in the Appendix). There was a statistical separation between two groups of birds around the overall mean SDP (i.e., the mean for all 17 birds combined, 0.69). The predicted values for eight of the birds (53.33%) were always smaller than that overall mean SDP; these include an immature white-backed vulture (tag ID 5785) and the immature hooded (tag ID CAT1). An effect of tag provider might also be visible as the Savannah tags (the tag ID starting with "st2010-") systematically showed higher values. This could be owed to the different sampling regimes in place and future work could address this point.

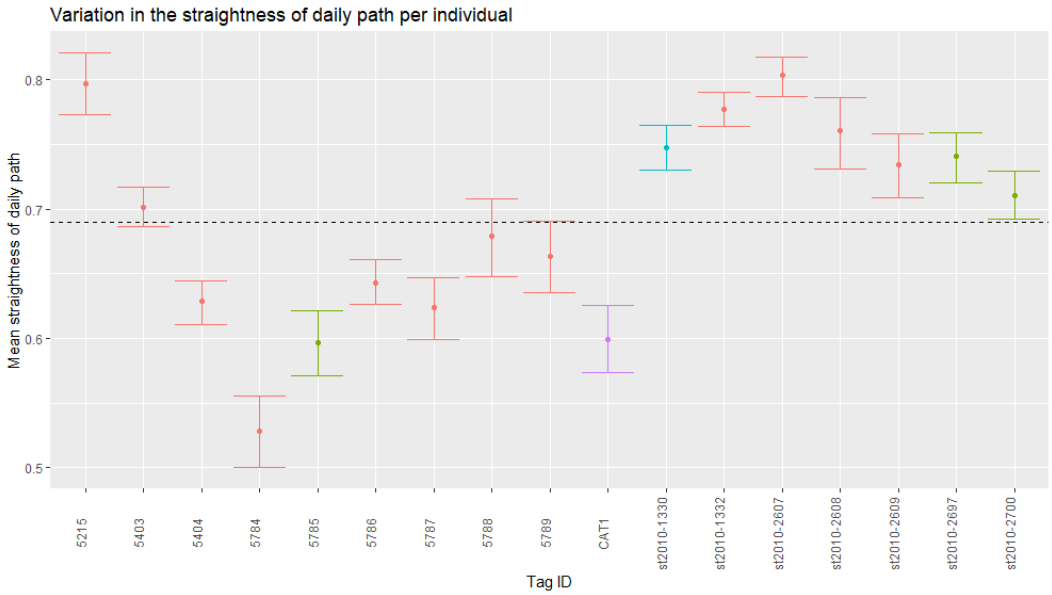


Figure 3-23 Variation in the straightness of a daily path for each individual generated by the best candidate model. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; adult hooded vulture in blue, immature in purple.

Additionally, the predictions generated from the second-best candidate model (*model TYS*, that with a negligible difference in the AIC score) showed potential temporal variation of the mean straightness of a daily path within individuals (**Figure 3-24**; **Table III. 10** in the Appendix). Despite the overlapping confidence intervals around each mean SDP along season for each bird, some genuine oscillation in the underlying mean may have been present in a few individuals, as was the case for birds with tag IDs 5404 and st2010-1332. Overall, the white-backed vultures displayed a variety of mean SDP profiles through time, with most birds displaying only a small change or an increase. The hooded vultures presented little variation but exhibits with a possible increase; the adult hooded vulture showed mostly higher mean SDP over time than the immature.

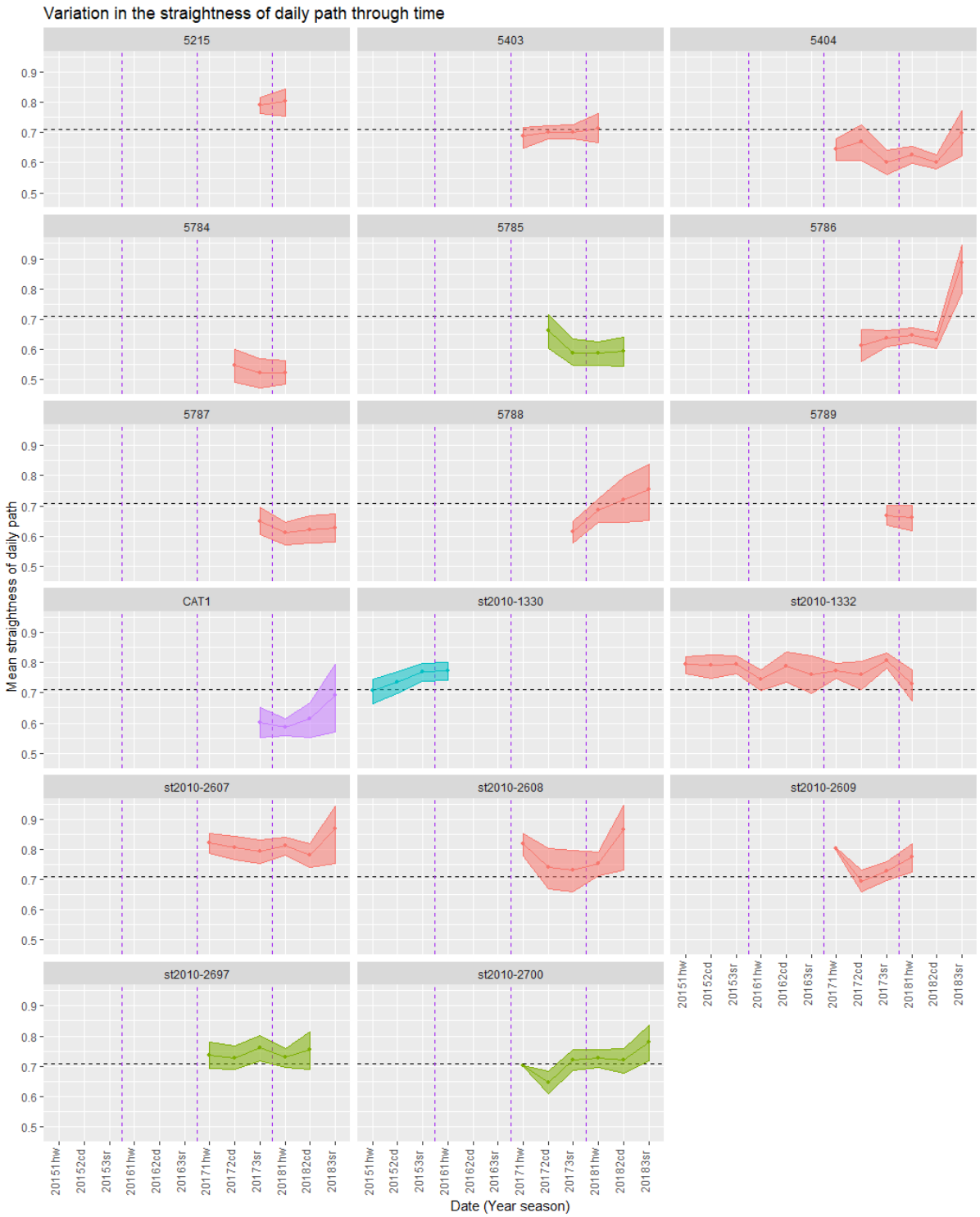


Figure 3-24 Variation in the straightness of a daily path (SDP) for each individual generated by the best candidate model. Mean predictions with respective 95% CI bands are shown. Individuals coloured by age class and species: adult White-backed vultures in red, immature and sub-adult in green; adult hooded in blue; immature hooded vulture in purple. Seasons are indicated with the respective year and shortened in the x-axis (Date) as: 1hw- hot wet, c2d- cold dry, 3sr- small rain. Dashed horizontal line represents the overall SDP mean. Dashed vertical lines separate the years.

The temporal variation of the minima and maxima seasonal mean straightness of a daily path was also perceptible. Generally, birds seemed to show the lowest expected mean SDP between January and May, during the hot wet season (**Figure 3-25**). Seven (41.18%) vultures had an expected minima SDP in that initial season; among these were four adults and one immature white-backed vulture, and both the hooded vultures. To note that the adult hooded as well as one of the adult white-backed (tag ID 5403) also have their maxima expected mean SDP during the hot wet season. As the year progressed the number of expected maxima and minima mean SDP even, to later show a large increase on the expected maxima SDP. During the small rain season (between September and December), 10 birds (58.82%) have an expected maxima SDP; among these were seven adults and two immature white-backed vultures and the immature hooded vulture. Two of those adult white-baked also had their expected minima mean SDP during the small rain season (tag IDs 5404 and 5788). Overall four birds (23.53%) had synchronous records of expected minima and maxima SDP within a season (**Table III. 10** in the Appendix).

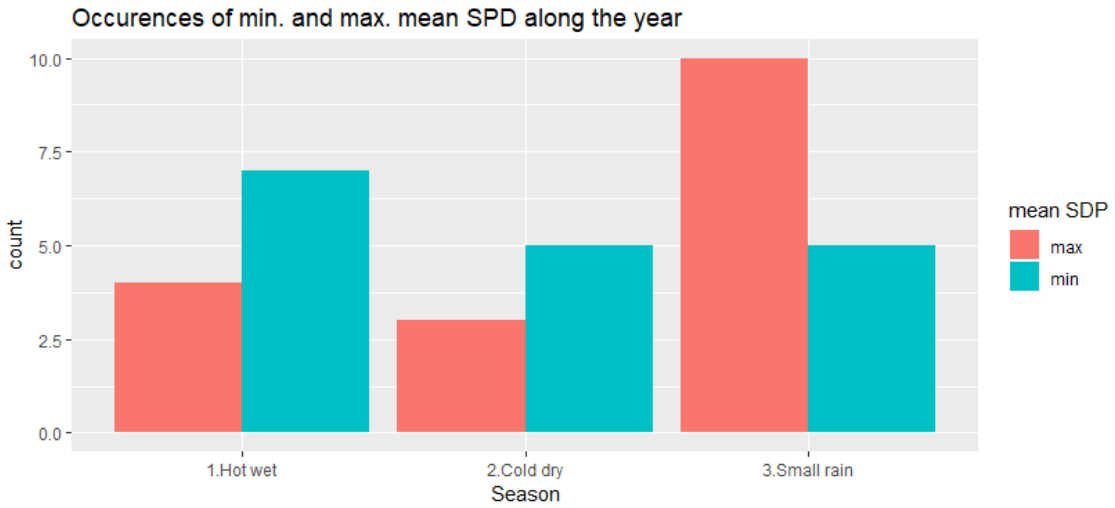


Figure 3-25 Summary of occurrence of the minimum (in blue) and maximum (in red) records mean straightness of a daily path(SDP) predicted for each bird. Seasons: 1.Hot wet - January to May, 2.Cold dry June to August, 3.Small rain – September to December.

3.3.5 Combined movement properties

Combined properties

Each of the individual properties provided some information about the pattern of movements a bird made in a day. Looking jointly at some properties might also bring additional information of biological relevance. For instance, did a vulture end a day far from its initial location that morning? Or rather, irrespective of how far a vulture flew away from its morning roost, did it return to spend the night close by? The ratio between the daily overall- and the maximum displacement may shed some light into these questions.

For example, if the overall displacement (DOD) was much smaller than the associated maximum displacement (DMD), then this indicates the bird visited far locations but then flew back towards where it first started. On the other hand, if the DOD metric was very similar to the DMD, this suggests the bird spent a great deal of time travelling in a direction away from the initial roosting location. On 11.66% of the days DOD represented no more than 10% of DMD, suggesting birds returned to a location not far from where they had started. This pattern was present in all birds, it ranged between 4.73 and 28.07% of their respective days, with four birds showing such movements on more than 16% of their days (two adult white-backed vultures and the two hooded). On the other hand, on 52.18% of days, the DOD represented at least 90% of the DMD, suggesting the birds roosted far from where they started that day. This pattern was also present in all birds, it ranged between 27.84 and 69.49% of their respective days, with four birds showing such movements on more than 64% of their days. These movements were present throughout all seasons, both with slightly higher proportions in the hot wet season than on the other two season (41.23 and 40.37%, respectively).

Furthermore, on just 4.71% of days did the vultures flew less than 1 km (DDT < 1 km). This may suggest birds always need to fly irrespective of the time of the year, and were only restrained from doing so on rare occasions (perhaps due to heavy rain or cold days). Despite the small representation, there was a greater proportion of these restricted movements during the hot wet season (47.91%), followed by the cold dry season (32.80%).

Additional biological questions

The *travellers* and the *locals*

Comparing multiple daily properties between birds may also uncover distinct movement strategies. For instance, did birds repeat their daily movements within one given area, or did they explore new areas?

The distances that each vulture reached farther away from their initial locations varied greatly, as described earlier on **Section 3.2.1**. Focusing on the white-backed vultures, those distances ranged between 141.74 km and 1,627.84 km. And in fact, three individuals did not visit locations more than 204 km away from where they were first seen, while three other distanced themselves more than 1,000 km. Furthermore, the index weighting those farther distances with the number of days each vulture was monitored for, also supports the separation of vultures in two sub-groups. Might these two distinct groups showcase distinct movement strategies?

Three birds were selected from each end of the range of values for the index to farther distances (**Figure 3-2**) in combination with the length of farther distance, to illustrate the contrast in the daily properties. The "locals", did not visit locations more than about 200 km from their initial location (birds with tag IDs 5784, 5785 (immature), and 5788; **Table 3-2**); they also showed a very low index to farther distances (**Figure 3-2**, to the left of the vertical dashed line). The "travellers" on the other hand, were seen more than 1,000 km away (birds with tag IDs 5786, 5789, and st2010-2700 (sub-adult)); **Table 3-2**) and their index to farther distances was high (**Figure 3-2**, to the right of the vertical dashed line).

Comparing the mean daily metrics between the birds in these two groups generated mixed results, regarding their particular values and the time of year in which they occurred (**Table IV. 1** in the Appendix). Intuitively one might think *travellers* fly larger distances each day, and assume these three birds would rank higher in terms of maximum daily distance travelled (DDT). DDT performed by the *locals* was nonetheless higher on average than that of the *travellers* (with only one instance where the confidence intervals slightly overlap). Furthermore, putting these six birds in context with the remaining nine white-backed vultures and inspecting the individual absolute maxima DDT, we see the *locals* ranked 2nd, 5th and 7th, whereas the *travellers* ranked 1st, 6th and 11th. This finding indicated that even though *locals* confined their movements to small geographical extents, they were also capable of flying similar distances in a day.

Contrasting the individual movement metrics between the two birds that ranked higher in terms of individual absolute maxima DDT (bird with tag ID 5786, a *traveller*, and tag ID 5785, an immature *local*) provided the results shown in **Table 3-4**. Even though there was a mixture on the mean metrics recorded for both birds for the total length of data for these individuals, some differences arose on an isolated day. On the day each bird performed its maxima DDT, both birds flew just over 400 km, the overall displacement from the *traveller* was only slightly higher but its maximum displacement was almost twice as that from the *local*. The latter showed a considerably lower SDP.

Table 3-4 Summary of the properties of the movement of the two birds that performed the largest distance travelled (DDT, km; 5786 and 5785). General information (top) as well as specific properties to those relevant dates (bottom) are presented. Mean, 95% confidence intervals (inside square brackets) and range (inside round brackets) are show. Distances as follow: daily distance travelled (DDT), daily overall displacement (DOD), daily maximum displacement (DMD), straightness of a daily path (SDP). Δ shows the difference in metrics between the two birds.

Metrics	Tag ID 5786	Tag ID 5785	Δ
overall summary			
Age class	adult	immature	
group	*traveller*	*local*	
Distance to farther most location (km)	1,127.71	141.74	985.98
summary of DDT (km)	101.75 [93.97;109.53] (0.01-429.17)	134.25 [125.81;142.68] (0.06-416.08)	
summary of DOD (km)	45.55 [40.51;50.59] (0-224.25)	45.98 [42.54;49.41] (0-142.96)	
summary of DMD (km)	53.43 [48.51;58.35] (0-225.29)	57.68 [54.36;61.01] (0.01-144.62)	
summary of SDP	0.65 [0.63;0.67] (0.18-1)	0.6 [0.58;0.62] (0.06-1)	
details from the day of largest DDT			
Date	2017-11-26	2017-11-13	
Number of locations	77	79	
DDT (km)	429.17	416.08	13.09
DOD (km)	37.43	27.48	9.95
DMD (km)	178.11	96.2	81.91
Mean SDP	0.79	0.51	0.28

The analysis so far has focussed on average metrics so to understand the differences found between birds on an isolated day, the movement patterns of the three *travellers* were investigated further, this time focusing on events of large DMD. Even though this was only a brief inspection, it was noticeable that the total distance flown in a similar time frame (e.g., a week) could vary strikingly (see **Table IV. 2** and **Figure IV. 1** in the Appendix, also for further description). This was illustrated by the bird with tag ID 5786 that recorded a maximum displacement of 622.39 km during 8 days (starting on the 2017-10-20), to then stay quite local with a maximum displacement of just 46.79 km the following week.

3.4 Discussion

This study provides a significant extension to the reports available at present in the literature regarding the daily movements of vultures. A small number of previous studies have measured daily metrics for white-backed vultures, although none formally assessed changes at different temporal scales. With respect to hooded vultures, the reports are even scarcer. All but two preceding studies have also not made spatial maps available which show the full geographical extent of the locations recorded, making comparisons with the present study challenging.

Visual inspection of overall movements

A visual inspection of the overall locations recorded in the present study suggested there was a variety of individual movement strategies. Some birds remained in smaller areas while others explored farther afield. The individual distribution maps varied considerably (individual maps shown in **Appendix II**). Some white-backed vultures stayed mostly local to Etosha National Park (NP) while others visited some of the neighbouring countries. One previous deployment of high resolution GPS transmitters was made in Etosha NP by Spiegel *et al*., generating several outputs [73, 76, 88]; four adult lappet faced vultures (*Torgos tracheliotos*) were monitored up to 512 days and 10 adult white-backed vultures up to 310 days, during 2008 and 2009 (see **Figure I. 2** and **Figure I. 3** in the Appendix). The study also showed vultures stayed mostly local to Etosha, further highlighting greater preference for the central and western sections of the Park [73]. Interestingly, the individual tracks for one of the white-backed vulture showed great similarity with some of the vultures in this study (e.g., the adult tag ID 5788, see **Figure II. 8**; and the immature tag ID 5785, see **Figure II. 5**), with birds exploring Etosha and territories to the south of the Park [88]. Coincidentally, one of the white-backed vultures (the adult tag ID 5786, see **Figure II. 6**) also showed similarity with the long path highlighted in the earlier study; birds explored the NW – SE section of Namibia performing a long-range foray ([88]; see also **Figure I. 2**, right hand side).

The tracks from this study also showed some similarities with the one other study, by Phipps *et al.* (2013) that deployed GPS transmitters on white-backed vultures. Six immature birds were tracked from the North West Province of South Africa for up to 313 days prior to 2012 (date not reported, [39]). Each bird showed different patterns of space use (see **Figure I. 4** in the Appendix **Appendix I**). Two vultures flew as far north as the Kavango-Zambezi Transfrontier Conservation Area (TFCA), where the two hooded vultures and two adult white-headed in the present study also spent time. For reference, the Kavango-Zambezi TFCA encircles the Bwabwata NP and extends through all neighbouring countries, i.e., Angola, Namibia, Botswana, Zambia and Zimbabwe [89]. One other adult

white-headed in the present study performed a long journey south; even though its tracks do not seem to show much similarity with the previous immature birds, it did show avoidance for the central regions of Botswana (tag ID 5789, see **Figure II. 9** in the Appendix). This was interestingly also observed by one other immature, as well as the sub-adult in the present study (tag ID st2010-2700, see **Figure II. 17** in the Appendix). Furthermore, this latter also visited that North West Province of South Africa (where deployments took place in [39]).

Overall, looking at all the white-backed vulture locations recorded in the present study, it was clear that there was a preference for the central-northern part of Namibia. The majority of that area is used for agriculture and tourism on freehold land, meaning there will not only be natural carcasses available but also remains from farming, hunting and abattoirs. There might therefore be a rich food source available for scavengers such as vultures. The avoidance for the northern strip can be explained by the fact that the land there is mostly used for small scale agriculture on communal land [90]; this means the local communities remove the wildlife carcasses, either for human consumption or for disposal if infected. Furthermore, it is also noticeable there is an avoidance in the farther-north, coinciding with the location of the two most densely human populated Namibian regions – the Oshana and the Ohangwena Regions [90]. With respect to the far northeast, the birds show a preference for the proximity of water bodies. The Okavango and Cuando rivers (in Angola, Namibia and Botswana) are prominent features of known outstanding value for wildlife [90].

With regards to the two hooded vultures monitored in this study, they both stayed locally around Bwabwata NP, with movements mostly within the Kavango-Zambezi TFCA. One recent study collated information from hooded vultures monitored via GPS transmitters over six African countries between 2013 and 2017 [91, 92], although no map has yet been made publicly available. The five birds monitored in Botswana showed differences in their space usage [92], and ranged “primarily over north-east Botswana (basically centred on Chobe National Park), but also into adjacent parts of Namibia, Angola, Zambia and Zimbabwe” [93], i.e., also keeping mostly within the Kavango-Zambezi TFCA.

Additionally, the present study also found that vultures could visit locations farther than previously reported. Even though the preceding study carried out in Etosha focused on long movements, the authors found white-backed vultures visited locations as far as 650 km to Southern Namibia [73]. The study that monitored six immature white-backed from the North West Province of South Africa found

those could reach as far as 900 km (in a maximum period of 301 days) from their place of capture [39]. The two immature white-backed in the present study did not reach as far; even though they were monitored for longer they only travelled as far as 230 km (in 336 days). Most interestingly though, is that despite the suggestion in the literature that immature *Gyps* vultures are thought to move over larger foraging ranges than adults [39], that was not the case in the present study. Three adults reached farther than 1,200 km up to a maximum of an unprecedented 1,628 km (recorded by the sub-adult in 188 days). Moreover, these farther points may have been reached during long-range movement known as "long-range forays" by birds that adapt to explore remote locations to exploit resources such as food patches (see for [73] review).

The two hooded vultures tracked in this study travelled up to 98.88 km (in 211 days). No comparative records were found in the literature, although this species is known to be generally sedentary [45].

Daily movement properties

The definition of the daily metrics analysed in this study followed on preceding work in Etosha which focused on the foraging efficiency of vultures [76]. The ten white-backed vultures showed slightly higher mean daily distances travelled with far narrower 95% confidence intervals, but all within the range of values obtained in the present study. The mean daily distance travelled (DDT) reported was 120.7 km (95% CI= 100.32, 141.08) contrasting to the present study 94.09 km (95% CI= 0.42, 256.83); the daily overall displacement was 44.20 km (95% CI= 39.10, 42.30) contrasting with 39.86 km (95% CI= 0.01, 157.42); the daily maximum displacement was 55.20 km (95% CI= 49.71, 60.69) contrasting with 48.77 km (95% CI= 0.12, 158.63). The differences in the width of the confidence intervals may be due to dissimilarities in the length of day considered as well as the longer duration of the monitoring in the present study. Comparatively, the study that monitored six immature white-backed vultures also reported daily distances travelled (DDT) [39]. Even though no overall average is provided, the individual mean DDT ranged between 22.27 km (95% CI= 18.10, 26.45) and 48.86 km (95% CI= 43.78, 53.94). These values are considerably lower than the ones found in the present study, although with overlapping 95% confidence intervals. Furthermore, the mean straightness of daily path reported in the preceding work in Etosha was slightly lower although the range of values was contained within those reported in the present study: 0.63 (95% CI= 0.60, 0.66) contrasting with 0.70 (95% CI= 0.27, 0.99) [76].

With regards to the hooded vultures, the mean daily properties recorded by the two individuals in the present study were lower than those recorded by the white-backed vultures, with only two exceptions. The mean DDT by one of the hooded vultures was similar to two other white-backed vultures, and the mean straightness of daily path for both hooded fell within those seen for the white-backed vultures. In addition, the five hooded vultures monitored in Botswana showed differences in the mean DDT [93]. Differences between day- and night time were detected although no differences between the wet and dry season [93]. The mean daytime DDT recorded during the wet season was 46.26 km (95% CI= 31.99, 60.53) very similar to the present study 46.44 km (95% CI= 0.51, 153.93), despite the wider confidence interval in the latter. Those contrasted with the mean DDT at night (during the wet season) of 0.25 km (95% CI= 0.07, 0.43). The findings support the species is generally sedentary, and more so at night [93]. Additionally, the significantly lower DDT at night may also reiterate that the contrasting confidence intervals between the present study and those being discussed, may be due to variations in the length of day analysed (either the length of data collection or the length of daylight).

The models used in this study allowed the detection of significant variations of some of the mean daily properties of the birds through time. Oscillations were visible in all birds although each bird exhibited its own pattern. It was possible to detect differences in the mean daily distance travelled (DDT) at a monthly level, and differences in mean daily maximum displacement (DMD) were only visible at a seasonal scale. In contrast, no significant temporal variation was detected for the daily overall displacement or the straightness of the daily path (DOD and SDP, respectively). Nonetheless, despite the overlap in the confidence intervals around the means for each bird, it was still possible to describe differences between individual birds (and within species) in terms of DOD and SDP. Additionally, the second-best candidate model showed significant variation in the mean SDP per bird between seasons.

The literature suggests vertebrates will forage farther when the abundance of resource is low, also with a reduced spatio-temporal predictability [94]. Vultures are known to have large foraging ranges and to travel long distances, indicating a sparse and unpredictable distribution of food resource (i.e. ungulate carcasses) [39, 95]. Also, the distribution of prey (prey abundance as well as prey mortality) has also been linked to the seasonal movements of African vultures [96]. Furthermore, foraging movements have also been suggested to be larger during the breeding season, when breeding pairs access feeding sites farther from the colony [97]. The literature though, referred to space usage over large periods of time (e.g. month). Only one other previous study assessed movement patterns on a daily level, having been unable to detect differences in the mean daily distances travelled between

the wet and dry seasons [98]. Even though the present study had no information about the breeding status of its birds, and it had very limited information about the distribution of food availability to vultures throughout its vast study area (see **Figure 5-1**), a few further remarks can be made:

All three daily properties for which it was possible to illustrate some significant temporal variation showed a common broad pattern of variation. A larger number of minima was seen as the year started (hot wet season, between January and May), followed by a smaller disparity between the number of maxima and minima during the cold dry season (between June and August), and later a sharp increase on the number of maxima (small rainy season, between September and December). The majority of the minima mean distances were consistently recorded during a hot wet season. This may have been due to environmental constraints such as temperature but also the rain tends to increase in this season, affecting the ability of birds to fly (*pers. obs.*). The richness in prey biomass as consequence of the rains may also provide enough food resources close to the roost. On the other hand, most the maxima mean distances were recorded during the small rainy season. At this time of the year it may be that prey is more scattered or not available in enough amount to sustain additional energetic needs in the case of breeding pairs nurturing a young. Furthermore, the temporal variation found for the SDP also agreed with the findings for the other metrics (DDT and DMD). The majority of minima occurred as the year starts suggesting a larger number of relatively erratic flights. Later, the majority of maxima in SDP occurred during the small rainy season, thus suggesting flights approximated perfectly straight paths, as the birds travel longer distances.

There were clear differences between individuals with birds displaying distinct movement strategies. Interestingly, 11 out of the 17 birds (64.71%) also showed synchronous minima and maxima on at least one of its daily properties (i.e., both minima and maxima were recorded during the same season). This may reflect a variation in the wet and dry seasons throughout the study area. Given the absence of a link between the daily properties and the geo-referenced locations where they were recorded, it may be that the underlying environmental conditions were driving the mixture of results found. In future analysis, it might be valuable to include a proxy for the weather that shapes the environment at a smaller scale (e.g., number of days since the last significant rainy period, at the location of each bird-day). Even though the number of locations analysed for the hooded vultures was far smaller than those available for the white-backed (less than 7.24%), it was still possible to illustrate the potential temporal variation in the daily properties for such species.

The best models selected to describe the temporal variation of the daily properties varied in their temporal scale. It was possible to discuss changes in the daily distance travelled at a monthly scale, but it was not possible altogether for the daily overall displacement (DOD). Moreover, three of the

candidate models for DOD failed to converge. Two factors may have contributed to this lack of convergence; on one hand the number of observations per correlation block was sometimes small (less than five), on the other hand there were cases when both minima and maxima DOD occurred synchronously, illustrating the large variance at play.

Combined properties

The results discussed above show that patterns of a single property are somewhat informative, but it may be that real ecological and biological value comes from interpreting those properties in a combined way. In ecological terms, the daily distance travelled (DDT) will give us an indication about how much ground a bird covers in a day, the daily maximum displacement (DMD) will tell us if a bird flies far away from home, and the daily overall displacement (DOD) can give us a feel for whether a bird sleeps in the same roost on consecutive nights.

On slightly more than half the days (52.18%) the DOD represented at least 90% of the DMD, suggesting the birds in this study roosted far from where they started that day. These movements were recorded throughout the year, but occurred more often in the hot wet season than on the other two season. This was the seasons when the lowest mean distances were recorded. That movement pattern may suggest that even though birds tended not to fly far, they could compensate by covering different ground each day which might well grant them access to sufficient resources. Also, even though infrequent, the birds in the present study performed long journeys, which could be a good illustration of what this proportion of DOD to DMD entails (see **Figure IV. 1** in the Appendix). Birds only remained very close to their initial location of the day (DDT < 1 km) on rare occasions. This may indicate birds always explored the surrounding area irrespective of the time of the year, and only seldom did not, perhaps in days of heavy rain. Moreover, the DOD metrics provided a distance from night to morning roost but did not give repeatability (i.e., multiple visits to the same location) after that; it may be interesting to extend this study to look at number of revisits to the same roost, monitor a relative direction of path between roost, or even assess activity within a given radius around a roost location (or time frame) of interest.

The straightness of a daily path (SDP) relates the displacement and the total distance travelled to the farthest location in a day. And it can give an indication of preferences between a bee-line or a more convoluted shape of movement. Each individual bird showed a large range of SDP values (*e.g.*, SDP for tag ID 5404 ranged from 0.15 to 1), suggesting birds covered a wide range of movement shapes.

However, the mean predicted SPD per bird was always greater than 0.5 indicating a predominance for flight mostly straight, either facing away or towards the roost.

It was also speculated that when analysing movement properties, one could start to tease apart birds that cover a large area from those that stay more locally. When contrasting the individual movement properties between *travellers* and *locals*, one would intuitively expect a large distance travelled would be associated to a large displacement. However, the maximum DDT recorded per individual was lower for the *travellers*. Examining the movement properties of the two birds that performed the largest DDT in more detail showed that on those particular days (of similar conditions) despite the similar total distance travelled, the maximum displacement was almost twice larger for tag ID 5786 (a *traveller*). This was also reflected in the higher SDP value which indicated a less tortuous flight. The overall displacement was slightly higher for tag ID 5786 but the striking difference nonetheless, is that tag ID 5786 travelled eight times farther away from where it was first seen as tag ID 5785 (a *local*) did. These surprising results brought forward two important considerations. One possibility was that it could reflect the life stage of each bird. Vulture tag ID 5786 was an adult but perhaps a *floater* (i.e., a non-breeding migratory adult [11]) or a young adult not yet sexually mature (note ageing birds in the field can be challenging; G. Shatumbu, *pers. comm.*), having the freedom to explore new grounds in terms of resource richness, roost with less competition, or viable breeding mates. Vulture tag ID 5785 on the other hand was an immature bird, perhaps not yet equipped with the confidence to fly too far from its initial location, but nevertheless, performing long, more serpentine-like flights and exploring fully the resources available locally. The second consideration was that perhaps birds changed their movement very frequently within the time frame analysed. That is to say, the information about the large variability in the daily properties was lost when summarized as a mean (per month or overall per bird). Our models allowed us to predict changes in month, season, or even just overall for each bird, but it may be that significant changes occurred in only a few days or weeks.

The duration of different “trips” performed by the *travellers* enabled the assessment of these ideas further. This highlighted that not only may there be great differences between birds, but also, and most importantly, that for a similar time period birds can show contrasting displacements. Vulture tag ID 5786 travelled highly variable distances in a similar time period (622.39 km in eight days followed by 46.79 km in six days). Spiegel *et al.* also found a lapped-faced vulture flew close to 1,000 km in only seven days [73]. Therefore, it is not surprising that it was difficult to tease apart different movement strategies, and it may perhaps be more informative to model mean metrics per week. Alternatively,

one could also try modelling the movement metrics in a quantile regression framework (i.e., analyse the patterns for the different quantiles such as for example, 95%, 50%, 5%).

To conclude, a suite of information has been combined and interpreted. Different time scales were examined- from bird locations (at least hourly), daily metrics, the predictions made for each month or season, to summaries per bird. Relevant movement properties were inspected, both separately and jointly. This generated new and meaningful insights on poorly known species with an urgently high conservation status. It has highlighted differences between individuals while also questioning whether immatures really do outperform adults in terms of long distances travelled.

This chapter has explored properties of movement proposed by preceding studies. Particularly it extended the knowledge of these aspects for white-backed vultures and presented the first descriptions for hooded vultures. Differences in movement properties through time have been perceived for all individuals but systematic patterns were not always clear. Differences in individual strategies have been identified and speculation has been made about the biological and ecological implications. More knowledge about the birds themselves would have been informative and it may be that the field protocols could be improved in the future in order to obtain such information. The findings presented in this chapter may also benefit from ground truthing and behavioural information. For example, to clarify the suggestions made about birds returning to a close location at the end of the day; or even to seek territoriality behaviour. Nonetheless, the results presented here may have direct application in small scale management and conservation plans, providing a detailed baseline about the variety of movements one can expect. Improvements to the statistical approach taken were also discussed. Lastly, movement properties are no doubt bound to a spatial element and this is explored in the following chapter.

4 Range areas - quantifying temporal and spatial shifts

In this chapter, the temporal scale of movement is considered at the monthly scale. Patterns of monthly range areas utilised by each vulture are described. Maps are generated to show the preferential areas (i.e., home range and core areas) used by each vulture, with associated uncertainty measures. Estimates of the size of those range areas are presented and the ratio of core area to home range for each bird is also discussed. Patterns of temporal and geographical variation are described and individual vultures are contrasted to demonstrate the individual variability observed. The findings in this chapter provide an unprecedented level of detail on the movement patterns of African vultures. Furthermore, the *floaters* are introduced.

Note: It is anticipated the publication of the results from the monthly range areas in a high impact movement ecology peer review journal to disseminate the approach taken and advocate for the need to use adequate methods that appropriately address the nature of geo-location data.

4.1 Introduction

“Home range” is a standard concept in animal ecology and behaviour and a crucial component of space use. Home range has been defined as the ‘‘area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.’’ [99]. This definition has been put forward in 1943 and it is the most widely referenced [100]. The typical goal of home range studies for ecology and conservation is the assessment of the total area required by the animals, the time spent in different areas within the home range, and the frequency of use of these areas [101]. This is often displayed in terms of a utilisation distribution, which is the relative frequency at which an animal uses different parts of its home range [101]. This in turn can help to identify the central area where an animal spends most of its time, denoted as core area; these can include important feeding and resting sites [101].

Historically, home range data was mostly obtained by recapturing marked individuals: the animals were captured, marked individually (e.g., with metal rings), and released at the location of original capture [102]. More recently, the advances in animal tracking technology and its growing use have

increased greatly our capacity to collect data to undertake home range analysis[3]. There is a variety of methods to estimate home range properties; those methods differ largely in the underlying assumptions about the positions of the individual during the intervals between recorded locations [6].

The analysis of home range has evolved from simple geometric methods such as delineating animal locations with a minimum convex polygon (MCP; [103]) to more complex statistical methods which account for the relative frequency distribution of those locations, namely using Kernel density estimators (KDE) [104]. Geometric methods such as MCP are still popular because they are easy to understand and to implement [100]. Other alternatives are being made more accessible for analysis through free software environments making KDE the method of choice [105] which is widely available via packages in R [62]. Specifically, studies often determine the cumulative 95% and 50% utilisation distribution, to represent an estimate of the size of the home range and core areas, respectively [106].

A key characteristic of geo-location movement data is that close observations (both in time and space) are likely to be correlated. While this correlation will decay in time, the autocorrelation in the data may persist over months or years [107]. Methods used in home range studies nonetheless rely on the assumption that observations are identical and independently distributed (IID). Failing to meet the IID assumption leads to underestimates of home range areas. This has been shown to be the case both for statistical and geometric methods [100]. Despite this discrepancy, well cited references (e.g. [108]), are still being extensively quoted as justification to neglect autocorrelation in recent studies [100]. To date, only one alternative has been derived to implement autocorrelated KDE (AKDE, [107]), available through the R package ctmm [109]. In a recent comparative study, among the candidate methods AKDE has been pointed as the only estimator able to generate accurate home range estimates on autocorrelated data [100]. Furthermore, that study found that methods which failed to address the IID assumption underestimated the home range sizes by a mean factor of two (i.e., estimates were on average half the real size).

Moreover, statistical estimates should also be accompanied by an associated measure of uncertainty, such as via confidence intervals. Even though confidence interval estimation is routine in nearly all other aspects of ecological research, this is so far largely omitted in home range studies [100]. The implementation of AKDE via the ctmm package is the only exception, with no other home range method providing a measure of error associated with its home range estimates [100].

The method implemented in this thesis adequately captures the autocorrelation structure of the data. The sandwich estimator was used to return robust standard errors [110], inflating the standard errors appropriately so that the estimates of uncertainty were appropriate. The panel structure used (bird-days) meant that locations within a day were correlated but between days were assumed to be

independent. The methodology is implemented in the freely available MRSea package [61] and all estimates are accompanied by an associated measure of uncertainty. Very few home range estimates are available in the literature for this study species for comparison, none of which account for the IID assumption.

Home ranges can be different between animals of different species, between individuals within a species, or even change over time within individuals [79, 111]. It is commonly assumed that home range size for vertebrates is inversely related to the abundance and the spatio-temporal predictability of resources [94]. Moreover, home ranges for large-bodied raptors can differ also according to individual reproductive status and be mainly regulated by habitat quality [112]. Golden eagles (*Aquila chrysaetos*) in the Mojave Desert (USA) show seasonal variation in home range size and in the use of vegetation classes which is thought to be tied to breeding status and environmental variation. In the summer, for instance, when temperatures increase they shift their home range uphill, from the desert to the mountains, to cool down [113]. Winter conditions with short and cold days provide unfavourable thermal conditions that too, deter vultures from crossing long distances [4]. Griffon vultures (*Gyps fulvus*) in the Grands Causses (France) differ in home range patterns between seasons, and show large variations between individuals both in terms of size, shape and position around the colony [12]. Bearded vultures (*Gypaetus barbatus*) tracked in the Pyrenees (Spain, France) also display differences in their home ranges as well as in daily movement [10]. Even though no differences were found between seasons, home ranges of this territorial species differed between age-class, and females for instance, performed greater distances than males. A detailed comparison of ranging patterns was made for territorial and non-territorial vultures, at spatial and temporal scales [10]. To name but a few examples.

Despite the growing number of home range studies being done on large raptors, some of which on vultures, studies of such nature in African species are still in their infancy. Satellite-based transmitters are being deployed but very few home range estimates are currently available in the literature.

This chapter focuses on patterns of the monthly range areas utilised by vultures to further describe the species movement ecology. The term “range areas” is used herein to refer to the general term of an estimate of a utilisation area with “home range” and “core area” being specific cases (as described in the Methods Section). The aims were to:

i) identify the preferential range areas each vulture visited per month, describing the respective home ranges and core areas with associated uncertainty measures;

ii) assess the temporal changes in the three metrics of monthly range areas, for each vulture: home ranges, core areas, and the ratio of core area to home range;

iii) examine the variation in the monthly range areas in terms of shape and geographic extent.

In particular, this chapter also investigates the flexibility of movements vultures displayed throughout their geographic range, with special emphasis given to the breeding season.

4.2 Methods

4.2.1 Data specification

The data analysed in this chapter was collected from satellite-based transmitters deployed on 16 vultures in Namibia (full details on **Section 2.2**). The time window for the blocks compared in these analyses was a calendar month. The expression “bird-month” is used hereafter to highlight that the months were treated as separate time blocks per bird. A bird-month, therefore, refers to all the georeferenced locations recorded for one vulture during one calendar month (e.g., “the first bird-month for vulture tag ID 5789” referred to all locations recorded for this bird during November 2017).

For the analysis of monthly range areas, only “bird-months” with sufficient data were investigated. As such, only months with vulture locations available for at least 10 days were included (**Table 4-1**). Additionally, tag ID 5215 was left out entirely given this individual only returned three months of data. The analysis used data transmitted between February 2015 and November 2018, providing locations for 16 vultures during 240 bird-months. The number of months analysed per bird ranges between five (tag ID 5789) and 35 (tag ID st2010-1332), with a mean of 15 months (**Table 4-1**). Each bird-month included data for 28.70 days on average; the number of days ranged between 11 and 31. The vulture locations were projected to the Universal Transverse Mercator (UTM) system to convert the coordinate units to meters. UTM zone 33 South was used as it best represents the study region.

Table 4-1 Details of the 16 vultures included in the study of home ranges. The transmitter identification (Tag ID) is shown as well as the deployment date, start and end date of recorded locations included in the analysis, number of days monitored (mean and range inside brackets), deployment area (NP = National Park), species and age class. White-backed vultures shown in black, hooded vultures in blue; sub-adult and immature highlighted in bold.

Tag ID	Deployment date	Start analysis	End analysis	Months monitored	Days per month	Deployment area	Species	Age class
5403	2017-04-11	2017-05-01	2018-03-31	11	29.55 (21-31)	Etosha NP	White-backed vulture	Adult
5404	2017-03-22	2017-04-01	2018-11-11	20	29.50 (11-31)	Kunene Region	White-backed vulture	Adult
5784	2017-07-18	2017-08-01	2018-03-30	8	30.25 (28-31)	Etosha NP	White-backed vulture	Adult
5785	2017-07-18	2017-08-01	2018-11-11	15	29.25 (11-31)	Etosha NP	White-backed vulture	**Immature**
5786	2017-08-19	2017-09-01	2018-10-23	14	29.86 (23-31)	Etosha NP	White-backed vulture	Adult
5787	2017-10-23	2017-11-01	2018-11-10	13	28.85 (10-31)	Bwabwata NP	White-backed vulture	Adult
5788	2017-11-02	2017-11-02	2018-11-11	11	25.91 (11-31)	Etosha NP	White-backed vulture	Adult
5789	2017-10-24	2017-11-01	2018-03-16	5	27.20 (16-31)	Bwabwata NP	White-backed vulture	Adult
CAT1	2017-10-24	2017-11-01	2018-11-11	13	28.92 (11-31)	Bwabwata NP	**Hooded vulture**	**Immature**
st2010-1330	2015-02-12	2015-03-01	2016-04-11	13	29.14 (11-31)	Bwabwata NP	**Hooded vulture**	Adult
st2010-1332	2015-02-16	2015-03-01	2018-04-10	35	26.17 (10-31)	Bwabwata NP	White-backed vulture	Adult
st2010-2607	2017-02-15	2017-03-01	2018-11-11	21	29.57 (11-31)	Etosha NP	White-backed vulture	Adult
st2010-2608	2017-03-11	2017-04-01	2018-11-11	17	27.76 (11-31)	Etosha NP	White-backed vulture	Adult
st2010-2609	2017-05-26	2017-06-01	2018-04-26	11	28.64 (14-31)	Etosha NP	White-backed vulture	Adult
st2010-2697	2017-04-22	2017-05-01	2018-07-26	15	29.20 (22-31)	Etosha NP	White-backed vulture	**Immature**
st2010-2700	2017-05-28	2017-06-01	2018-11-11	18	29.39 (11-31)	Etosha NP	White-backed vulture	**Sub-adult**

4.2.2 Home range and core areas

Model structure

One model was fitted for each bird-month separately. The identification of the monthly home ranges and core areas for each bird was based on the (cumulative and relative) probabilities of vulture presence within the respective geographic area. Those probabilities were modelled using Bernoulli Generalised Additive Models (GAMs, [21, 54]) as a function of the geographical coordinates (projected to UTM 33 S, easting and northing, in meters, herein referred to as the "spatial term"). The spatial term was included as a bivariate smooth.

Pseudo-absence locations were randomly generated from within the respective available area. The geographic areas available for each bird-month were defined as the minimum bounding rectangle (MBR) within which all the respective monthly vulture locations lie. The rectangles were oriented in a North-South and East-West direction. There were as many MBRs as "bird-month". For each vulture location (presence), five pseudo-absences locations are drawn (see **Section 2-15** for further explanation).

GAMs for longitudinal data can be described as Generalised Linear Model (GLM) with a linear predictor defined by a sum of smooth functions of covariates. The models used here (for each bird-month) can be expressed as:

$$g(E[Y_{it}]) = \beta_0 + f(x_{east.\ it}: x_{north.\ it}),$$

where Y_{it} is the response variable for a given bird at time t, the presence or absence of a bird i at time t, can be written as $Y_{it} \sim Bernoulli(1, p_{it})$, where p_{it} is the probability of bird presence for bird i at time t. β_0 represents the intercept. $f(x_{east.\ it}: x_{north.\ it})$ is a bivariate smooth of the spatial term constructed using, in this case, a Gaussian radial basis function [22] for bird i at time t. The mean variance relationship for Bernoulli variables is known in that $Var\ (Y_{it}) = p_{it}(1 - p_{it})$; and the linear expression is achieved by a link function $g(\cdot)$, here the logit function, expressed as

$$logit\ (p_{it}) = \log(p_{it}/1 - p_{it}).$$

Model Setup

The bivariate smooth of the spatial term for these models was based on the CReSS method (Complex REgion Spatial Smoother, [60]) with SALSA2D to determine the number and location of knots (the flexibility of the smooth, [22]).

Candidate knot locations were set out, evenly spaced (via a space-filling algorithm) through the monthly geographical range available for each bird (as defined above). SALSA2D was used to choose the final allocation of knots and their effective range and the parameters for SALSA2D were:

- total number of candidate knots = 300,
- minimum knots = 2,
- maximum knots = 20,
- selection criteria: BIC,
- gap parameter = 0.

The method used for these models, respects the longitudinal nature of the data and acknowledges that the autocorrelation inherent to animal locations violates the residual independence assumption typically assumed. To allow for the residual correlation, a sandwich estimator was used to return robust standard errors [110], which inflates the standard errors appropriately so that the estimates of uncertainty shown here allow for the positive residual correlation likely to be present. The panel

structure used for all models (i.e. time window permitted to contain correlated residuals) were bird-days. This meant that residuals associated with locations within a day were permitted to be correlated but residuals between days were assumed to be independent. Naturally, these assumptions were thoroughly examined to ensure reliable estimates of uncertainty about the bird-month specific, home range and core area estimates.

Model selection and assessment

The flexibility of the bivariate smooth term was determined using the Bayesian Information Criterion (BIC, [84]) and the suitability of the correlated block was inspected using autocorrelation function (ACF) plots, within which the correlation inside each block was expected to decay to zero, on average. Further diagnostics included contrasting the estimated probability of vulture presence as well as the estimated range areas, with the respective recorded vulture locations.

Predictions and cumulative probabilities

Predictions from each of the final models (one for every bird-month) were generated onto grids of cells with 5x5 km, for each geographic area available for each bird-month (MBR). The uncertainty around the predictions was based on a sandwich estimates of variance and realised using a parametric bootstrap of the parameter estimates (model coefficients) and the robust variance-covariance matrix. The process was repeated 1,000 times to generate 1,000 sets of bootstrap predictions and create percentile-based confidence intervals.

Owing to the 5:1 generation of pseudo-absences to presences, the absolute value of the predictions does not reflect probabilities of presence, and so the relative probability of presence was instead presented which is calculated by dividing each predicted probability by the sum of the probabilities estimated for the entire prediction area (referred to as “relative p(pres)”).

The range areas for each vulture-month were calculated as follows. For the core area, the relative p(pres) were sorted in decreasing order and the cumulative sum was determined. The core area was defined as all the grid cells that encompassed the top 50% of the vulture presence for a given bird-month. The home range was defined as all the grid cells that encompassed the top 95% of the vulture presence for a given bird-month. The uncertainty surrounding each estimated range area was captured using a parametric bootstrap from the model described above and recalculating the home

range and core area for each realisation. 95 % confidence intervals were then calculated based on the 2.5 and 97.5 quantiles of the 1,000 bootstrap-based estimates of home range and core area.

Maps were generated for each bird-month showing the three relevant contours: the lines connecting the cells that made the expected mean home range or core area, and the lines connecting the cells that were included in the lower and upper 95% confidence limits. The size of each range area was calculated by multiplying the total number of cells included, by 25 sq.km (since each square was 5x5 km).

To further assess how vultures utilised each monthly range area, the ratio between the core area (CA) and the home range (HR) was also inspected. If a vulture showed a homogeneous spatial distribution one would expect a resulting ratio of 0.56 (CA/HR = 50/95 = 0.56).

All modelling was done with the MRSea package v. 1.0.1 [61] in R version 3.6.0 [62], with RStudio v. 1.1.456 [85]. Plotting was done with the ggplot2 [87] and fields [114] packages in R. All code will be provided with the associated journal publication.

4.3 Results

One model was fitted for each bird-month separately, resulting in estimates for 240 monthly range areas for the 16 vultures considered in this analysis. Overall, the models performed well, the correlation block used (bird-day) was adequate, and the estimated probability of vulture presence as well as the estimated range areas overlaid suitably with the respective recorded vulture locations. **Figure 4-1** illustrates this for the adult white-backed vulture tag ID 5876, during May 2018. The ACF plot shows a good decay of the correlation on average (shown by the red line) also inside each daily block; the lag shows the number of data points present in each block, in this case, between 456 and 468 data points were analysed per day (**Figure 4-1 A**). The estimated relative probability of presence across the geographic areas utilised in this bird-month overlap suitably with the respective vulture locations recorded (**Figure 4-1 B**). And the areas included (shown in red) and excluded (in blue) from the home range (**Figure 4-1 C**) and core area (**Figure 4-1 D**) highlight the cells with higher probability of vulture presence as defined (95% of the cumulative probabilities for home range and 50% for core area).

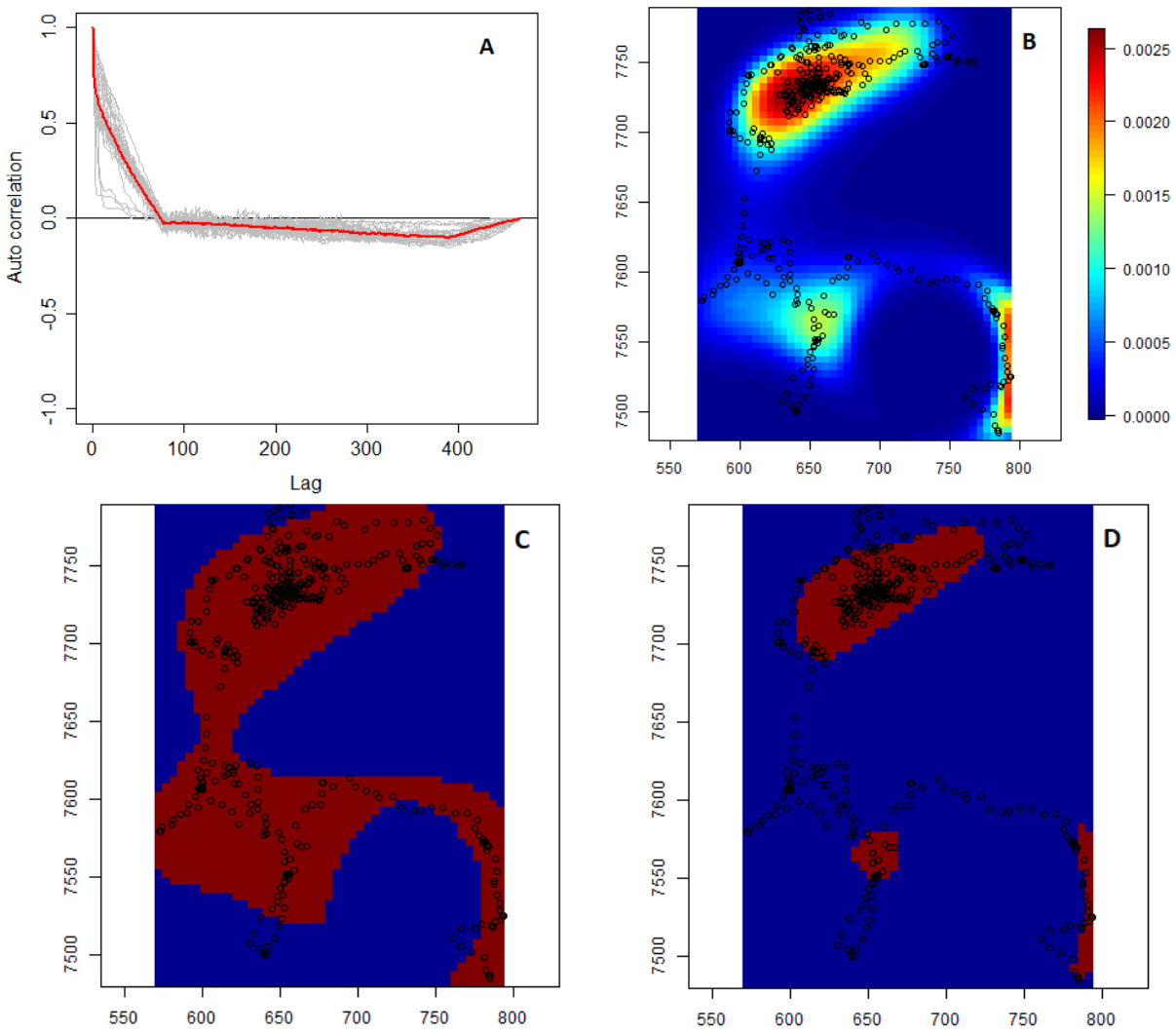


Figure 4-1 Illustration of the diagnostics performed to assess each model fit, to each bird-month. These plots refer to the white-backed vulture ID 5876, during May 2018. A- autocorrelation function (ACF) plot shows a good decay of the correlation on average (red line) at the end of each correlation block (lag shows the number of observations inside each block); B- estimated relative probability of presence; C- estimated mean home range for this month shown in red; and D- estimated mean core area for this month shown in red. Vulture locations are shown in circle black points.

4.3.1 Size of range areas

Home range, core area, and ratio of core area to home range

The mean size of monthly home ranges for white-backed vultures (here represented by 14 individuals, two of which were immature and another a sub-adult), far exceeded that of the hooded vultures (represented by one adult and one immature, **Table 4-2**; see **Figure 4-2**, and **Table V. 1** in the Appendix, for results for each individual). Both the mean home ranges and core areas were at least 10 times larger for the white-backed vultures. Nonetheless, there was individual variability between all

birds and the two groups of species showed an overlapping 95% confidence interval (CI) indicating that there may not be a genuine difference between the species.

The ratio of core area to home range however, was not that disparate between the two species (**Table 4-2**). The ratio was only slightly smaller for the hooded vultures, which also exhibited a wider 95% CI.

Table 4-2 Summary of the size of each estimated range area per species/ individual. Details for each individual vulture are illustrated in the figure below and shown in the **Appendix V**. The number of months per bird is shown (taken as the sum of the respective *n* individuals). The mean size of range areas (home range (HR), and core area (CA), thousand sq.km) are shown with 95% confidence limits (CI) (inside square brackets) and range values (round brackets). The ratio of core area to home range (CA/HR is also shown with 95%CI and range values.

Species	Number of months	HR (thousand sq.km)	CA (thousand sq.km)	CA/ HR
White-backed vultures (n=15)	214	24.75 [2.38; 107.62] (1.17 - 145.45)	6.50 [0.47; 28.29] (0.25 - 48.53)	0.25 [0.16; 0.33] (0.12 - 0.52)
Hooded vultures (n=2)	26	1.87 [0.49; 4.40] (0.37 - 4.46)	0.45 [0.07; 1.41] (0.05 - 2.01)	0.23 [0.13; 0.39] (0.13 - 0.52)

Examining the metrics described above for each individual vulture, it was noticeable there was a large variability both between and within vultures (**Figure 4-2**). Overall, home ranges were three to five times larger than the core areas, also evidenced in the ratio of core area to home range which sits mostly between 0.20 (= 1/5) and 0.33 (= 1/3). Two white-backed vultures (adult with tag ID 5796 and the sub-adult tag ID st2010-2700) show the largest variability in home range and core areas. Conversely, three other adult white-backed and two immature display much lower variability in areas (tag IDs 5784, st2010-1332, and st2010-2608; and 5785, and st2010-2697, respectively). The smallest inter-quantile ranges, lowest variability, were from the two hooded vultures.

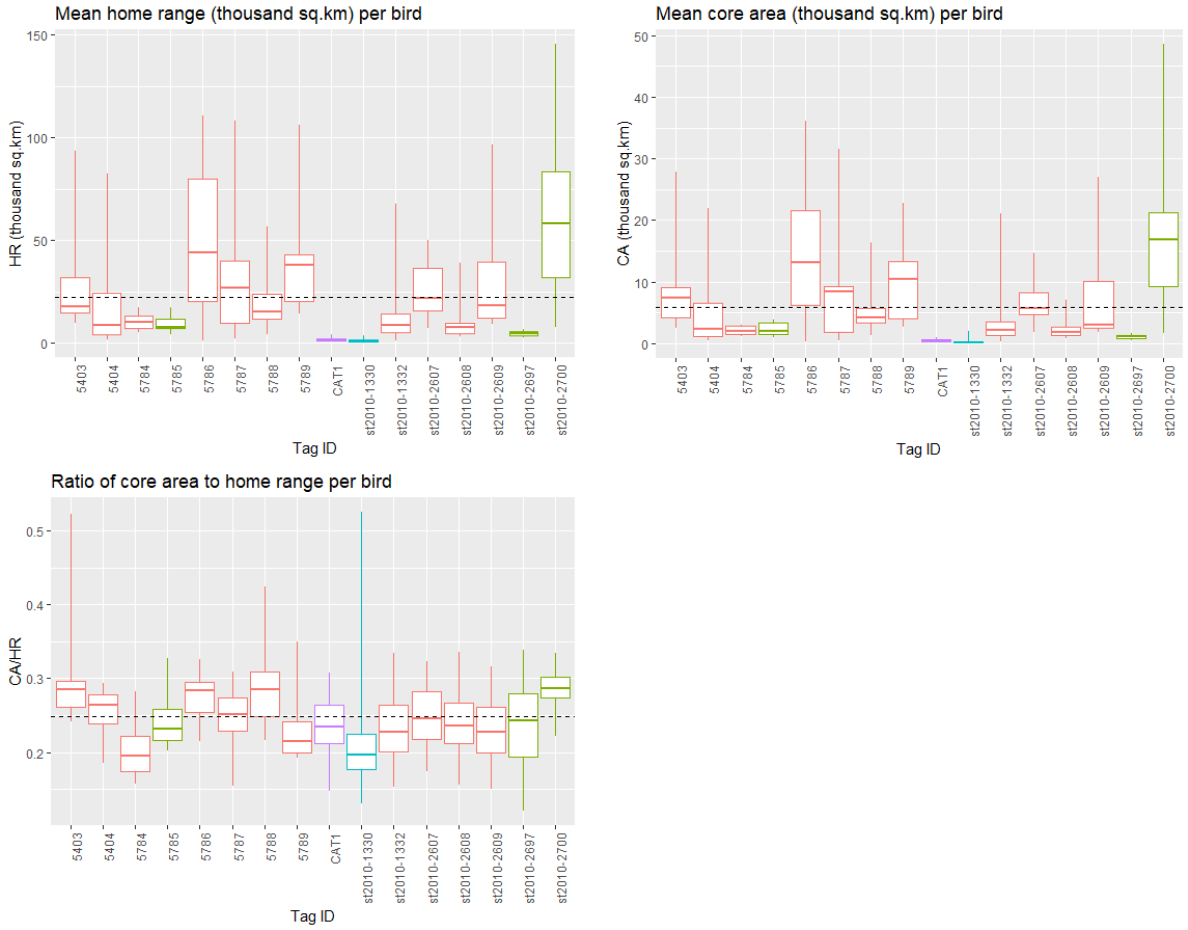


Figure 4-2 Variation in each measure of the monthly range areas for each bird. Box plots show the 25% (bottom), 50% (middle) and 75% (top) quantiles, as well as the minimum (extent of the lower line) and maximum (extent of the upper line) values. Colours represent species and age classes: light red – adult white-backed, green – sub-adult and immature white-backed, blue – adult hooded, purple – immature hooded. The horizontal dashed line in each plot shows the mean metric for all birds combined, for reference.

4.3.2 Temporal variation in range areas

Home range and core area

Large variation in the size of range areas was also evident through time. The size and variability between individuals was such that the oscillations through time are represented in four separate figures (**Figure 4-3** to **Figure 4-6**). Individuals were grouped according to the magnitude of the range areas, and each figure has its own range of sizes; this allows the pattern for each bird to be well visible (note the range areas reach 150 thousand sq.km (th.sq.km) on **Figure 4-3** but are smaller than 8 th.sq.km on **Figure 4-6**).

Displaying the home ranges and core areas in the same plot further illustrates that even though core areas fluctuate through time, those fluctuations were less prominent that those observed for the

home ranges (**Figure 4-3** to **Figure 4-6**). The white-backed vultures tag ID 5784 (adult) and tag ID 5785 (immature) showed very little variation in the size of the core area through time, while the home ranges varied moderately (**Figure 4-6**, two plots on the left hand side). On the other hand, the white-backed vultures tag ID 5786 (adult) and tag ID st2010-2700 (sub-adult) showed noticeable fluctuation in the size of both home ranges and core areas (**Figure 4-3**, top left hand side and bottom right hand side plots). Moreover, even though the hooded vultures explore far smaller areas, the size of those also oscillates as time went by (**Figure 4-6,** two plots on the left hand side).

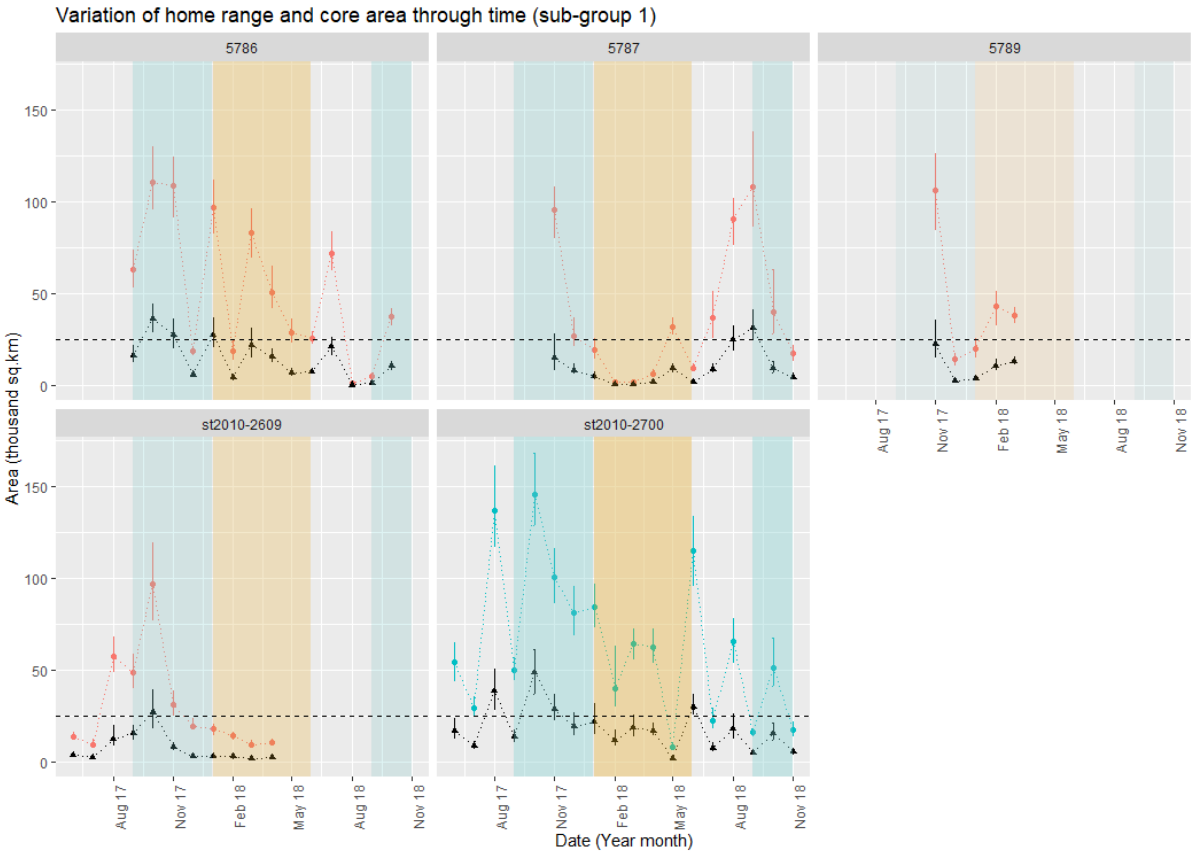


Figure 4-3 Temporal variation of home range and core area size, for a sub-group of birds. Mean values are shown with the 95%CI limits. Size of range areas shown in thousand sq.km, home range shown in circles, and core areas in triangles. Subset presented of five adult white-backed vultures that show larger range areas (tag ID 5786, 5787, 5789, st2010-2609, and st2010-2700). Individuals coloured by age class and species (for home range): adults in red, and sub-adult in light blue Seasons along the year highlighted differently: hot wet in golden, cold dry in grey, small rain in blue. The horizontal dashed line in each plot shows the mean range area for these birds combined, for reference.

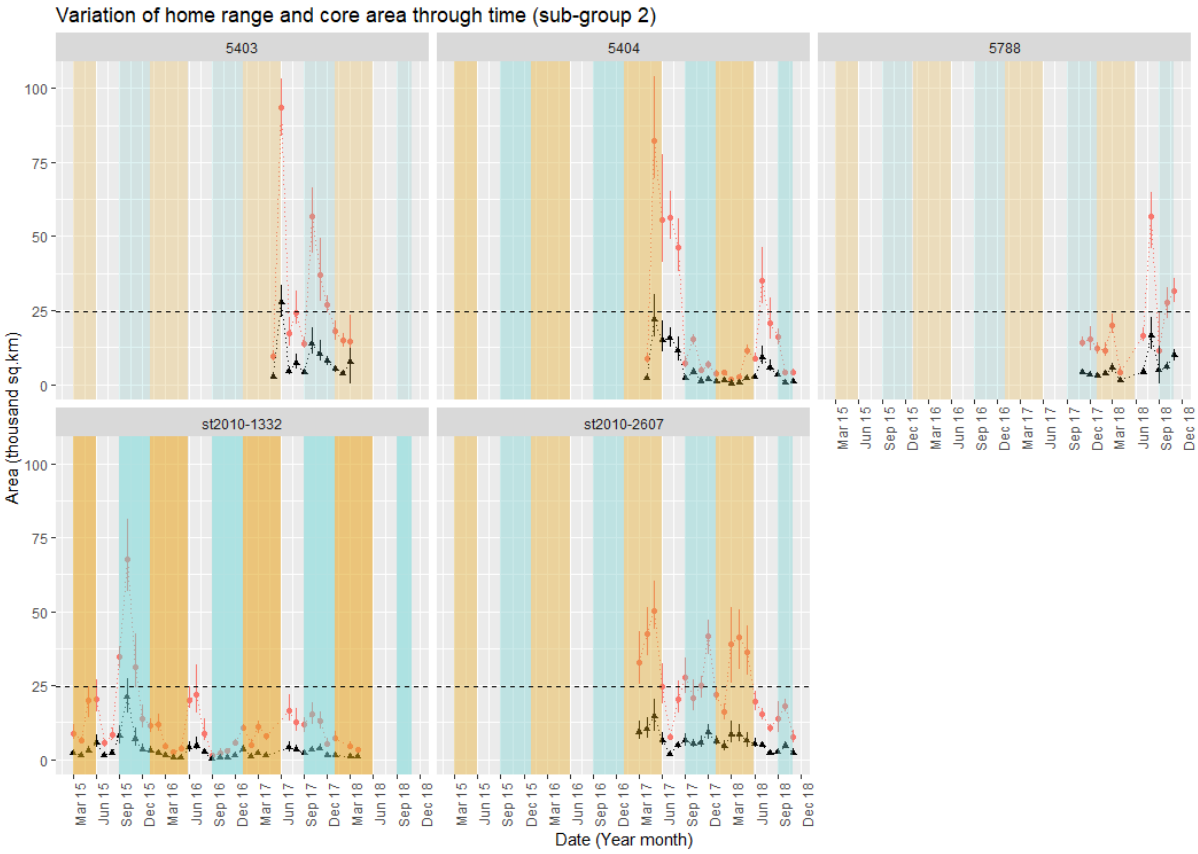


Figure 4-4 Temporal variation of home range and core area size, for another sub-group of birds. Mean values are shown with the 95%CI limits. Size of range areas shown in thousand sq.km, home range shown in circles, and core areas in triangles. Subset presented of five adult white-backed vultures that show the second larger range areas (tag ID 5403, 5404, 5788, st2010-1332, and st2010-2607). Seasons along the year highlighted differently: hot wet in golden, cold dry in grey, small rain in blue. The horizontal dashed line in each plot shows the mean range area for these birds combined, for reference.

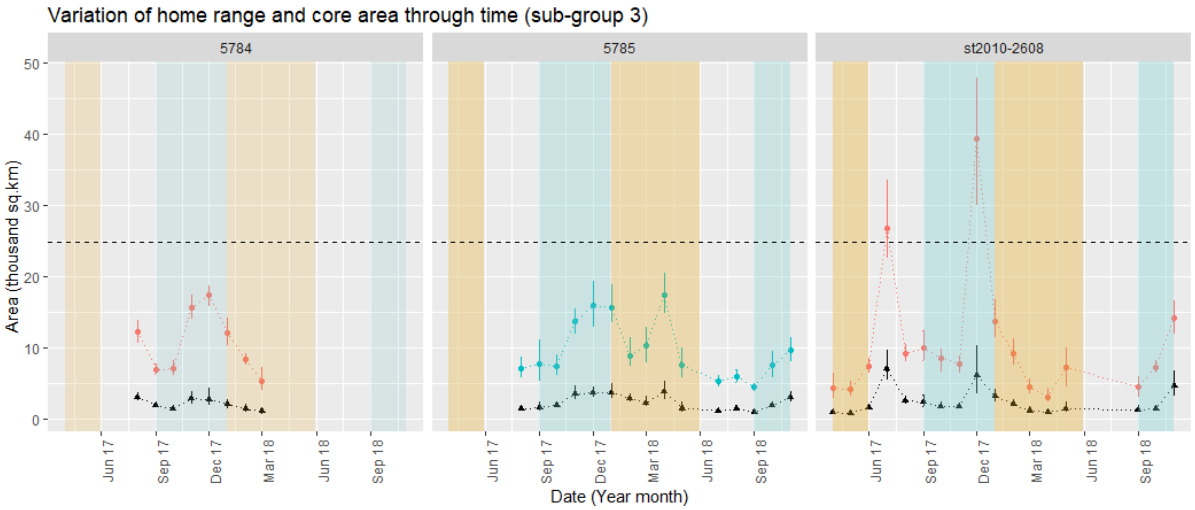


Figure 4-5 Temporal variation of home range and core area size, for another sub-group of birds. Mean values are shown with the 95%CI limits. Size of range areas shown in thousand sq.km, home range shown in circles, and core areas in triangles. Subset presented of three white-backed vultures that show smaller range areas (tag ID 5784, 5785, and st2010-2608). Individuals coloured by age class and species (for home range): adults in red, immature and sub-adult in light blue. Seasons along the year highlighted differently: hot wet in golden, cold dry in grey, small rain in blue. The horizontal dashed line in each plot shows the mean range area for these birds combined, for reference.

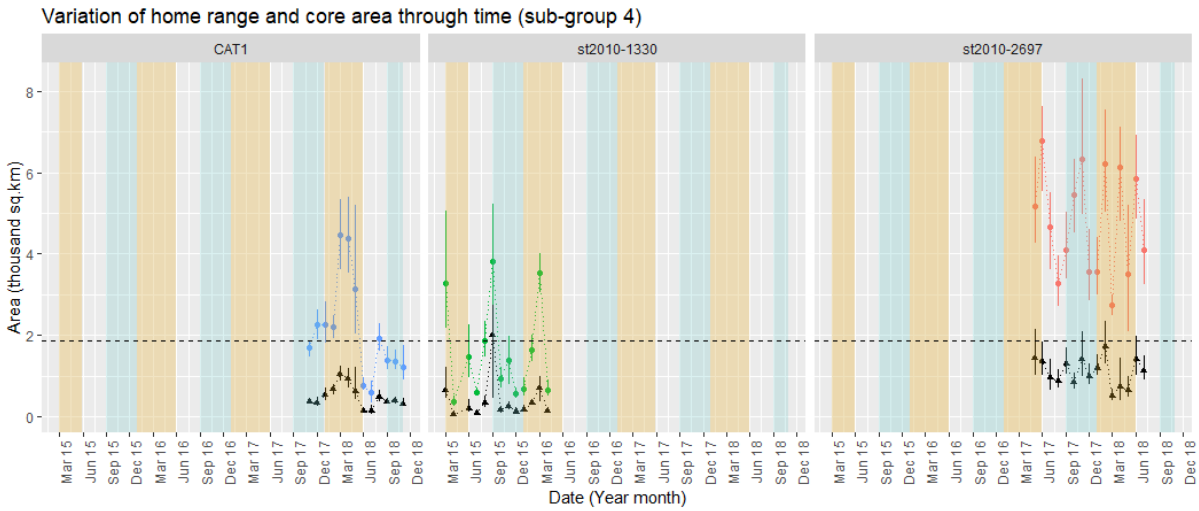


Figure 4-6 Temporal variation of home range and core area size, for the last sub-group of birds. Mean values are shown with the 95%CI limits. Size of range areas shown in thousand sq.km, home range shown in circles, and core areas in triangles. Subset presented of three vultures that show the smallest range areas (tag ID CAT1, st2010-1330, and st2010-2697). Individuals coloured by age class and species (for home range): immature hooded vulture in blue; adult hooded in green; immature white-backed in red. Seasons along the year highlighted differently: hot wet in golden, cold dry in grey, small rain in blue. The horizontal dashed line in each plot shows the mean range area for these birds combined, for reference.

There was a distinct difference in the timing when the minima and maxima mean monthly home range size occurred (**Figure 4-7**, and **Table V. 2** in the Appendix) across individuals. No extreme values took

place in the first two months of the year, but a peak of minima mean home range occurred in March (five vultures, 31.25%). Adding the occurrences in April (3) and May (2) made a total of 10 vultures (62.50%) that recorded their minima mean home range during the hot wet season. Among these were nine white-backed vulture (seven adults, one immature, and the sub-adult), and the adult hooded vulture. Three minima were recorded during the subsequent cold dry season (one of which from the immature hooded vulture), and three more on the last season of the year (between September and December).

The peak of maxima mean home range occurred in October (four vultures, 25.0%; **Figure 4-7**, and **Table V. 2** in the Appendix). One maxima recorded in November and another two in December made small-rain the season with highest records of maxima mean home range (total of nine birds, 56.25%); these included eight white-backed vultures (one of which the sub-adult) and the adult hooded. There were four maxima during the hot wet season (one of which from the immature hooded vulture), and the remaining three maxima occurred between June and August (cold dry season). Three birds had both their minima and maxima during the same season (18.75%).

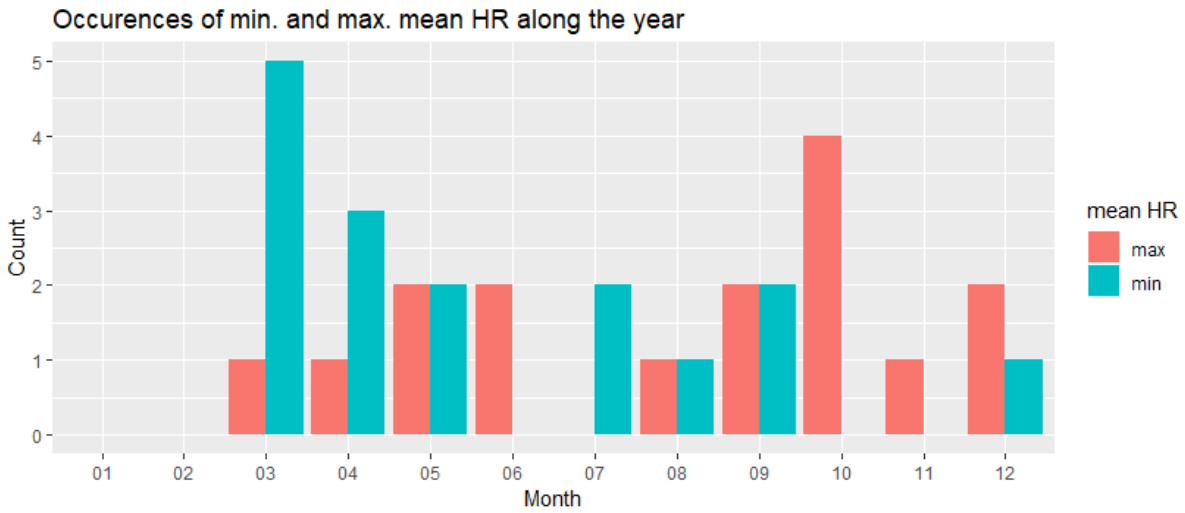


Figure 4-7 Occurrence of the minima (blue) and maxima (red) mean monthly home ranges (HR) recorded along the year. All birds are present, note each coloured count will sum to 16.

The temporal variation of the minima and maxima mean monthly core area size was also perceptible (**Figure 4-8**, and **Table V. 3** in the Appendix). Both peaks of minima and maxima core area size occurred at the same time as those for the home range (March and October, respectively). As above, 10 minima mean core area size took place during the hot wet season and those records belonged to the same

individuals (nine white-backed and the adult hooded vulture). The remainder six records of minima core area size were evenly present in the two consecutive seasons of the year. The immature hooded vulture had its minima during the cold dry season.

Even though the peak of maxima mean core area size was synchronous to the peak of maxima home ranges, the counts distributed slightly different along the year (**Figure 4-8**, and **Table V. 3** in the Appendix). Five maxima records took place during the initial season of the year (hot wet, 31.25%), one of them belonging to the immature hooded vulture. Four other birds had their maxima mean core area size between June and August (25% and all adult white-backed vultures). The higher number of maxima occurred during the small rain season with seven birds showing their largest core area size then (43.75%, the immature hooded vulture being one of them). Four birds had both their minima and maxima during the same season (25.00%); three of those birds were the same that recorded synchronous minima and maxima mean home ranges.

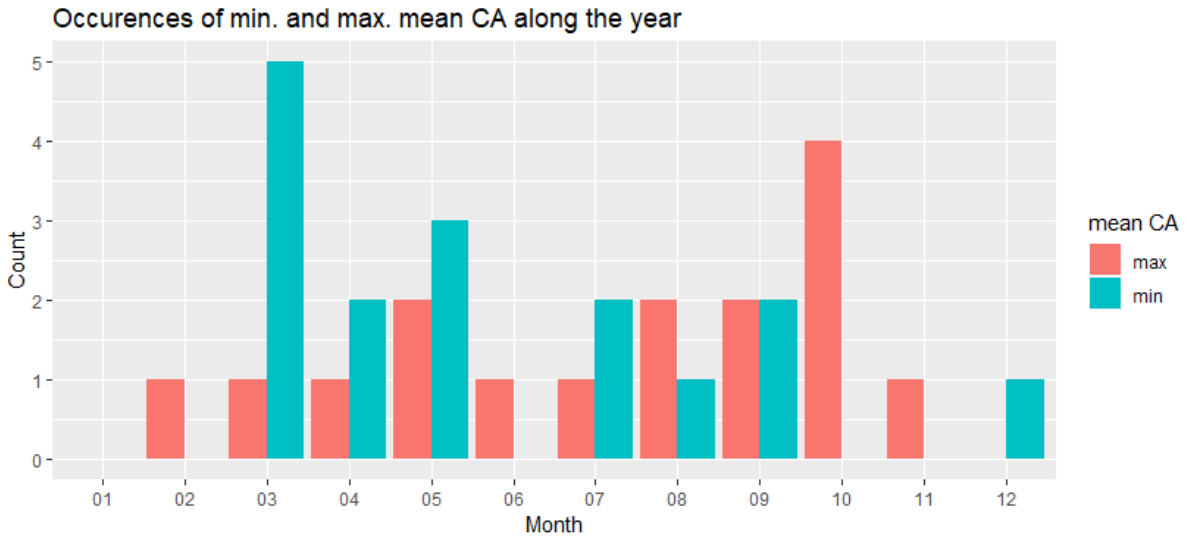


Figure 4-8 Occurrence of the minima (blue) and maxima (red) mean core areas (CA) recorded along the year. All birds are present, note each coloured count will sum to 16.

Ratio of core area to home range

The estimated mean ratio across all birds was 0.25 which was well below the 0.56 value expected if vultures distributed themselves homogeneously. This indicates that birds utilised their range areas in a notably patchy way.

Figure 4-9 also shows noticeable temporal variation in the monthly ratio of core area to home range size although it was not too pronounced. Each vulture showed its pattern of fluctuation through time. The absolute minimum was recorded in April 2008 by the immature white-backed vulture with tag ID st2010-2697 (0.121 [95% CI = 0.075; 0.213]). In turn, the adult hooded vulture recorded the absolute maximum in September 2015 (tag ID st2010-1330, 0.525 [95% CI = 0.517; 1.000]). The adult white-backed vulture with tag ID 5403 also shows a high upper 95% CI of 1.000, recorded in March 2018 (0.522 [95% CI = 0.200; 1.000]). These two high upper limits were partially omitted in **Figure 4-9** to allow the visualization of all other measures; all remaining upper 95% CI were lower than 0.524 and thus the range of the y-axis was cut at 0.6.

Figure 4-9 Temporal variation of the monthly ratio core area to home range size, for each vulture. Mean values are shown with the 95%CI limits. Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; adult hooded vulture in blue; immature hooded in purple. Seasons along the year highlighted differently: hot wet in golden, cold dry in grey, small rain in blue. The horizontal dashed line in each plot shows the mean range area for these birds combined, for reference.

The temporal variation of the minima and maxima monthly ratio of core area to home range (CA/HR) size was also evident (**Figure 4-10**, and **Table V. 3** in the Appendix). There was more fluctuation than in the temporal variation for the range areas separately, with more occurrences of the ratio at the beginning and the end of the year. Even though there were no minima recorded during February or March, the peak seen in May brought the number of minima ratio CA/HR to six during the hot wet season (37.50%, all 14 white-backed vultures). Only one minimum took place in July (from the immature hooded vulture), with no other records during the cold dry season. Lastly, two other peaks of occurrence in October and December made this the most popular season for the minima monthly ratio CA/HR; nine minima were recorded then (56.25%) one of which by the adult hooded vulture.

The number of maxima monthly ratio CA/HR also occurred mostly at the beginning and the end of the year (**Figure 4-10**, and **Table V. 3** in the Appendix). The number of records was in fact, the same during the hot wet and the small rainy seasons. Seven birds (43.75%) showed their maxima ratio CA/HR during each those seasons; the immature hooded was represented in the former, the adult hooded vulture in the latter. The two remaining records took place during July, by one adult and the sub-adult white-backed vultures. Eight birds had both their minima and maxima ratio during the same season (50.00%).

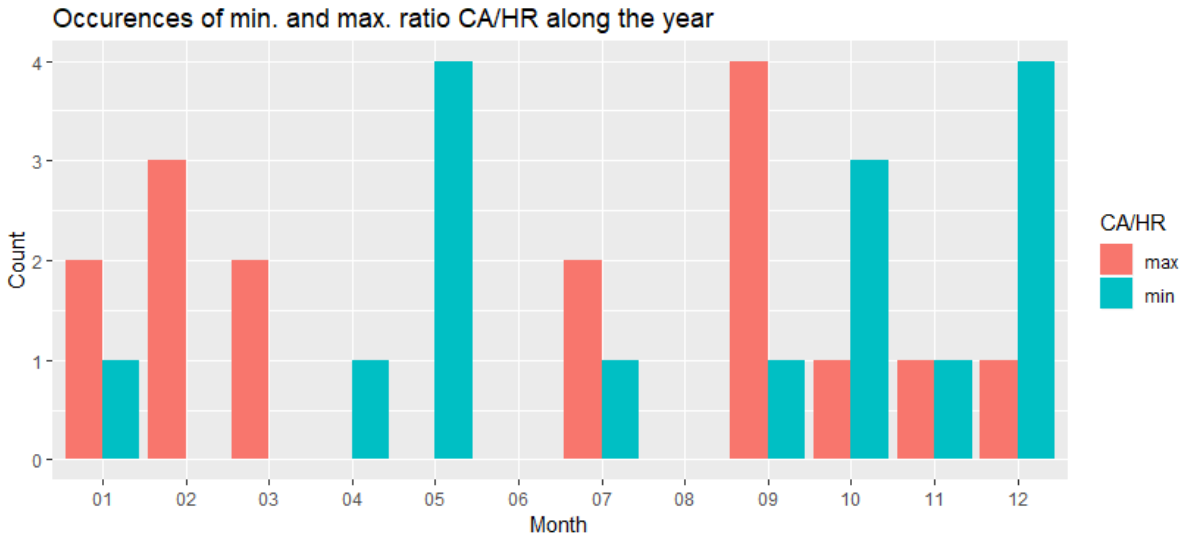


Figure 4-10 Occurrence of the minima (blue) and maxima (red) ratio core area to home range (CA/HR) recorded along the year. All birds are present, note each coloured count will sum to 16.

Additional biological questions

The *travellers* and the *locals*, revisited

Two vultures were selected to contrast extreme scenarios in the variation of range area sizes. One vulture held the smallest variation in the mean monthly home range, i.e., the smallest difference between the maximum mean and the minimum mean home range. The adult white-backed vulture tag ID 5784 was such bird, with a variation in the mean home range of 12.06 thousand sq.km (th.sq.km). The second vulture selected held the largest variation in the mean monthly home range. This was the sub-adult white-backed vulture tag ID st2010-2700, with a variation in the mean home range of 137.69 th.sq.km. Earlier in **Section 3.3.5**, vulture tag ID 5784 was labelled as a *local*, and vulture tag ID st2010-2700 as a *traveller*. To put these numbers into context, St Andrews has an area of 4.97 sq.km, almost 2.5 thousand times smaller than the smallest variation in home range; also, Aveiro has an area of 197.60 sq.km, almost 700 times smaller than the largest variation in home range.

Figure 4-11 and **Figure 4-12** show the size of the home range and of the core area, jointly with the ratio between those metrics for each of the two vultures selected, a *local* and a *traveller*. The horizontal dashed line in those figures shows the mean home range for all 16 birds combined (22.27 th.sq.km) and puts these two scenarios in context. The vulture tag ID 5784 showed a mild fluctuation of the size of the monthly home ranges, accompanied by a gentle fluctuation of the respective size of the core areas (**Figure 4-11**, top section). The ratio of core area to home range showed a visible drop as the home range increased, although the 95%CI of the monthly estimates overlapped (**Figure 4-11**, bottom section). The mean ratio for this *local* vulture was 0.21 [95%CI = 0.16; 0.28].

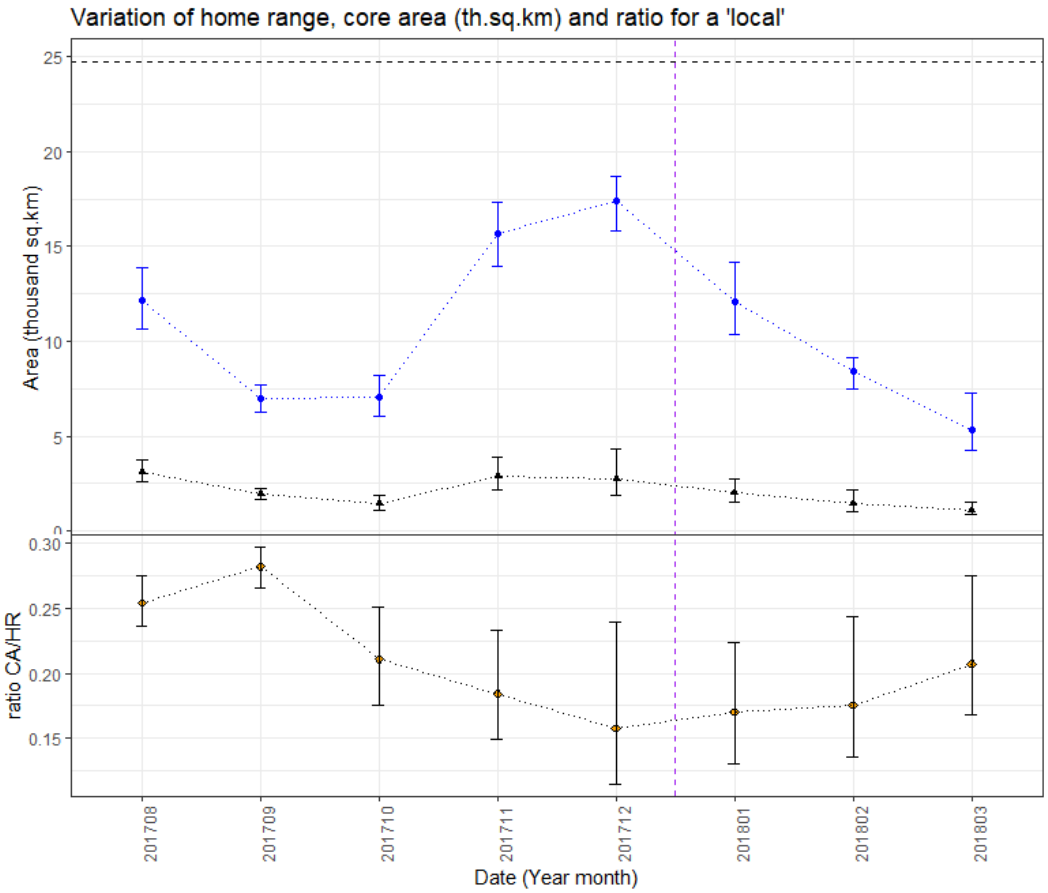


Figure 4-11 Mean monthly home range (blue circles), core area (black triangles; thousand sq.km; top section) and ratio of those metrics (orange diamonds, bottom section) for the bird with the smallest variation in the mean home ranges (the adult white-backed vulture, tag ID 5784). Mean values are shown with the 95%CI limits. The horizontal dashed line shows the mean home range for all 16 birds combined, and the purple vertical line separates years – to help interpretation.

In turn, the sub-adult white-backed *traveller* (tag ID st2010-2700) showed an irregular fluctuation of the size of the monthly home ranges, with some sharp variation between consecutive months (**Figure 4-12**, top section). Nonetheless, despite the visible oscillation in the respective size of the core areas, this was far less accentuated. Additionally, and most interestingly, the ratio of core area to home range showed variation but it was contained within a narrow range of values (**Figure 4-12**, bottom section). The mean ratio for this *traveller* vulture was 0.29 [95%CI =0.23; 0.33], not that distant from the ratio seen for the contrasting *local* vulture.

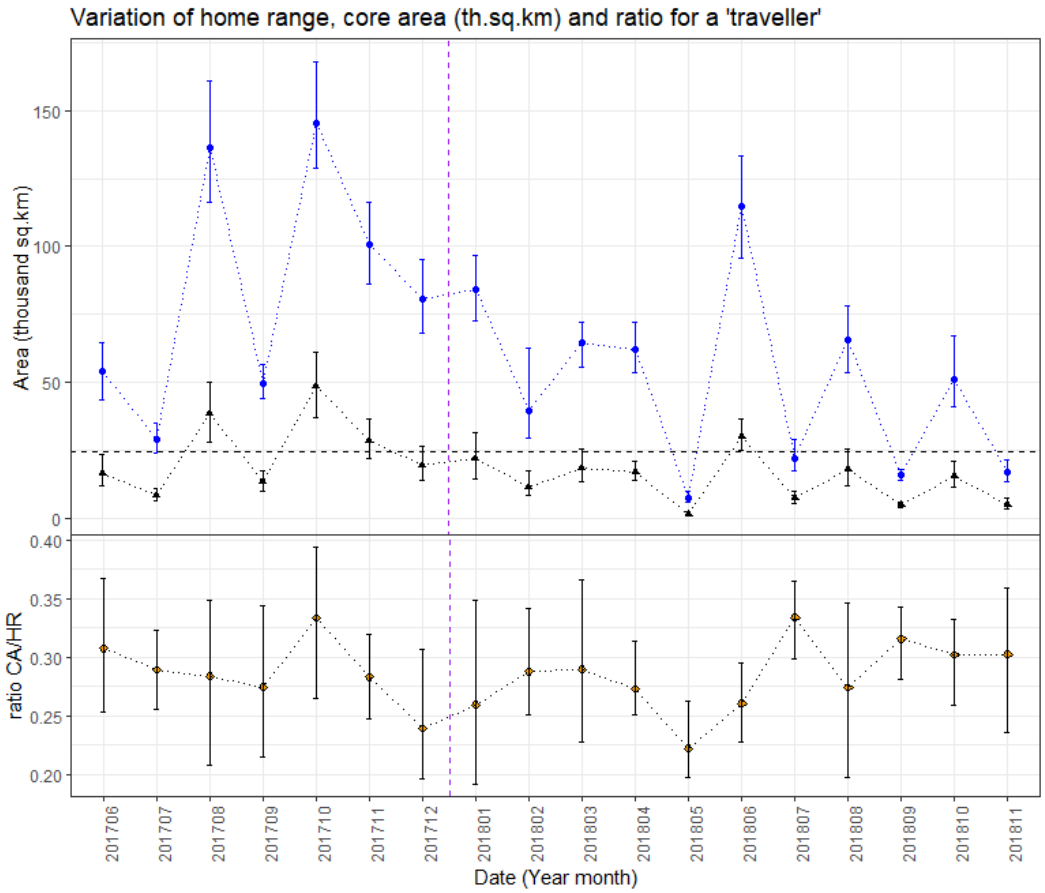


Figure 4-12 Mean monthly home range (blue circles), core area (black triangles; thousand sq.km; top section) and ratio of those metrics (orange diamonds, bottom section) for the bird with the largest variation in the mean home ranges (the sub-adult white-backed vulture, tag ID st2010-2700). Mean values are shown with the 95%CI limits. The horizontal dashed line shows the mean home range for all 16 birds combined, and the purple vertical line separates years – to help interpretation.

4.3.3 Spatial variation of range areas

Home range

The individual maps show clear differences in both the shape and the geographic extent of the monthly home ranges vultures utilised (areas encompassing 95% of the cumulative probabilities and respective 95% CL; **Figure VI. 1** to **Figure VI. 16** in the Appendix). Overall, vultures started the calendar year with a smaller home range and then expanded their range considerably in the second half of the calendar year. Each bird nonetheless showed its own monthly and annual variation. The *traveller* adult white-backed vulture was selected this time, to illustrate some of the spatial variation observed (tag ID 5786, **Figure 4-13**).

The vulture tag ID 5786 showed a different shape of home range for each of the 14 months (**Figure 4-13**). The areas with 95% of the (cumulative and relative) probability of presence changed location

through the entire geographic range of this bird. The adult white-backed vulture showed the tighter contraction in home range during August 2018 (1.175 th.sq.km [95%CI = 0. 375; 2,301]; **Table V. 2** in Appendix) staying very local around an area South of Windhoek. The maximum expansion occurred during October 2017 (110.664 th.sq.km [95%CI = 95,674; 130.206]; **Table V. 2** in Appendix) over an area that extended all the way north towards the northeast of Etosha National Park (NP). For reference, the area of Etosha NP (shown in the dashed line on the maps) is 22.270 th.sq.km. Not only did the geographic pattern changed from month to month, it also differed between years. Note for example, the two top left maps were quite different from the two last on the bottom right (**Figure 4-13**).

Lastly, note also that when a contour was not displayed as a closed line, this was due to visualisation and analysis using the minimum bounding rectangles. The estimated relative probabilities of vulture presence were occasionally challenging to plot as the area became very large.

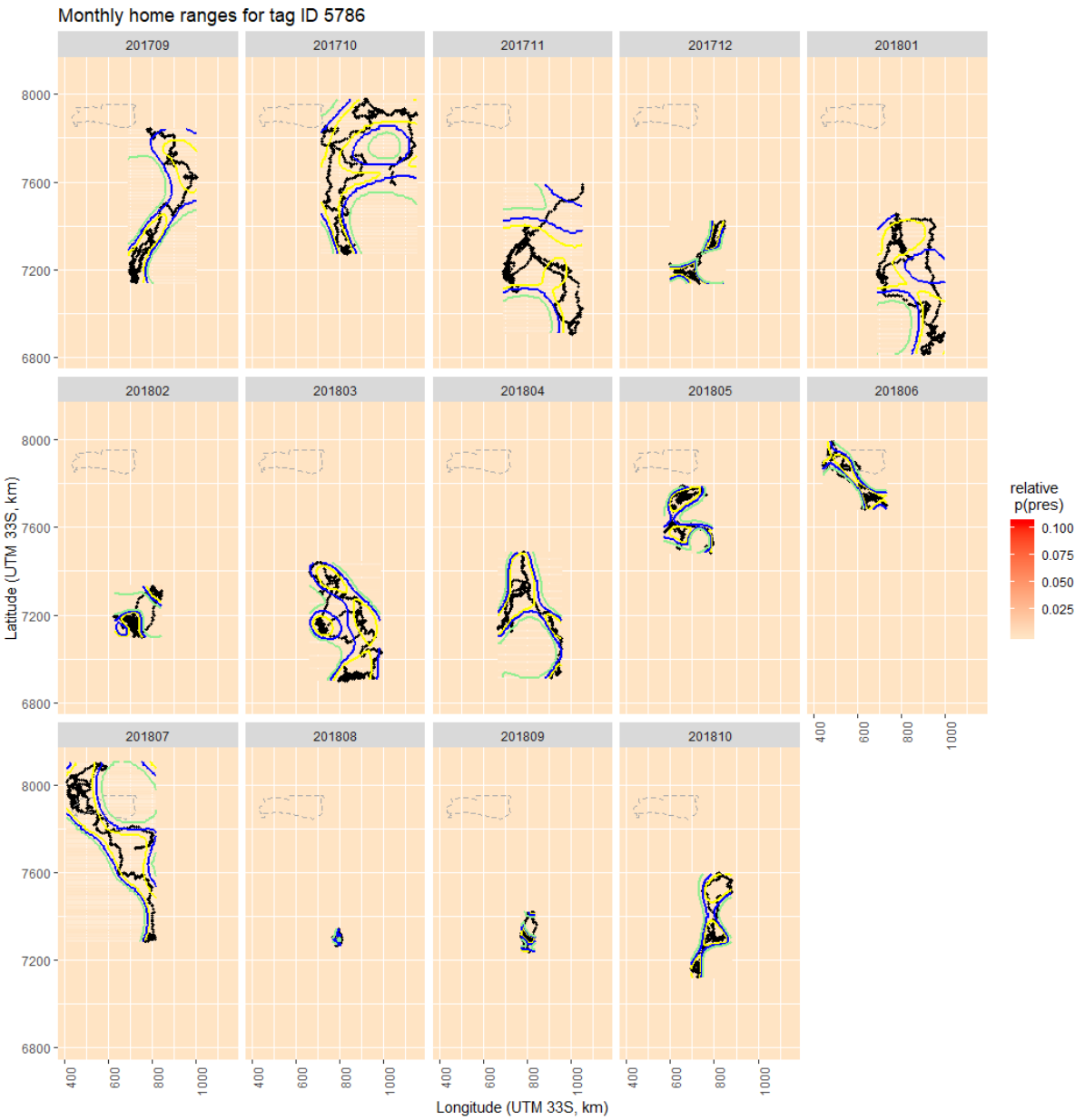


Figure 4-13 Variation in the mean monthly home range in terms of geographic location, shown with the relative probabilities of presence (in red gradient) and vulture locations (black dots). Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

The flexibility of movements vultures displayed is further illustrated. The months with tighter contraction and wider expansion for the same two birds selected above are contrasted (the most extreme cases of all birds; **4.3.2Figure 4-11** and **Figure 4-12** in the see previous Section). The *local* adult white-backed vulture tag ID 5784 showed the smallest variation in the mean monthly home range; the *traveller* sub-adult white-backed vulture tag ID st2010-2700, the largest variation.

The *local* adult white-backed vulture (tag ID 5784) had its largest monthly home range area during December 2017 (**Figure 4-14**, top left; 17.41 th.sq.km [95%CI = 15.83; 18.68], taken from **Table V. 2** in the Appendix) and its narrowest during March 2018 (**Figure 4-14**, top right; 5.34 th.sq.km [95%CI = 4.22; 7.28]). Both areas were located within Etosha National Park (NP), shown in the maps in the dashed line. In turn, the *traveller* sub-adult white-backed vulture (tag ID st2010-2700) displayed a remarkable variation in its monthly home range area. The wider expansion of monthly home range took place during October 2017 (**Figure 4-14**, bottom left; 145.45 th.sq.km [95%CI = 128.72; 168.01], taken from **Table V. 2** in the Appendix); the tighter contraction during May 2018 (**Figure 4-14**, bottom right; 7.76 th.sq.km [95%CI = 5.85; 10.10]). This vulture travelled far beyond Etosha NP, through an area larger than half the size of the United Kingdom (242.50 th.sq.km), and more than one and a half times larger than Portugal (92.09 th.sq.km).

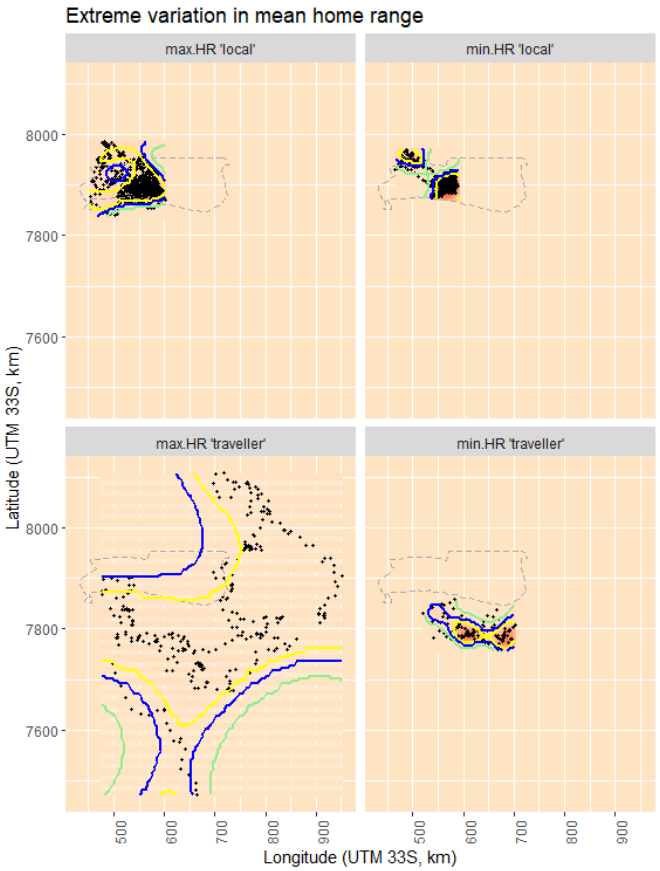


Figure 4-14 Variation in the mean home range in terms of geographic location, for four contrasting months, shown with the relative probabilities of presence (in red gradient) and vulture locations (black dots). Top: maximum (left) and minimum (right) expansion displayed by the *local* adult white-backed vulture tag ID 5784, which shows the smallest variation in the mean monthly home range. Bottom: maximum (left) and minimum (right) expansion performed by the *traveller* sub-adult white-backed vulture tag ID st2010-2700, with the largest variation in home range. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

Core area

Similarly, the individual maps for monthly core area also showed clear differences in both its shape and geographic extent (areas encompassing 50% of the cumulative probabilities and respective 95% CL; **Figure VI. 17** to **Figure VI. 32** in the Appendix). Each bird showed variable patterns of expansion and contraction, also showing differences between years. In keeping with the previous section, the same *traveller* adult white-backed vulture was selected to illustrate some of the spatial variation observed (tag ID 5786, **Figure 4-15**).

The core areas occupied clearly distinct parts of the geographic range of this bird. The most compact monthly core area took place during August 2018 (0. 35 th.sq.km [95%CI = 0. 05; 1.05], **Table V. 3** in the Appendix) with only the upper 95% CI limits perceptible in the map (**Figure 4-15**, bottom, second map on the left). The largest amplification of the monthly core area took place during October 2017 (36.03 th.sq.km [95%CI = 28.57; 44.56], **Table V. 3** in the Appendix) with three smaller areas united by the upper 95% CI contour (shown in green in the maps). For reference, the area of Etosha National Park (shown in the dashed line on the maps) is 22.27 th.sq.km.

The changes in geographic pattern from month to month, as well as the difference between years were more noticeable than in the case of the home ranges. Often the mean core area included non-contiguous areas, i.e., it was formed by smaller areas that did not touch. Two such cases occurred in January (**Figure 4-15**, top right map) and March 2018 (**Figure 4-15**, middle row, second map on the left). Three smaller areas were seen in January (shown in blue), also non-united by the upper 95% CI (shown in green). In March however, there were four smaller areas, two of which were joined by the upper 95% CI contour.

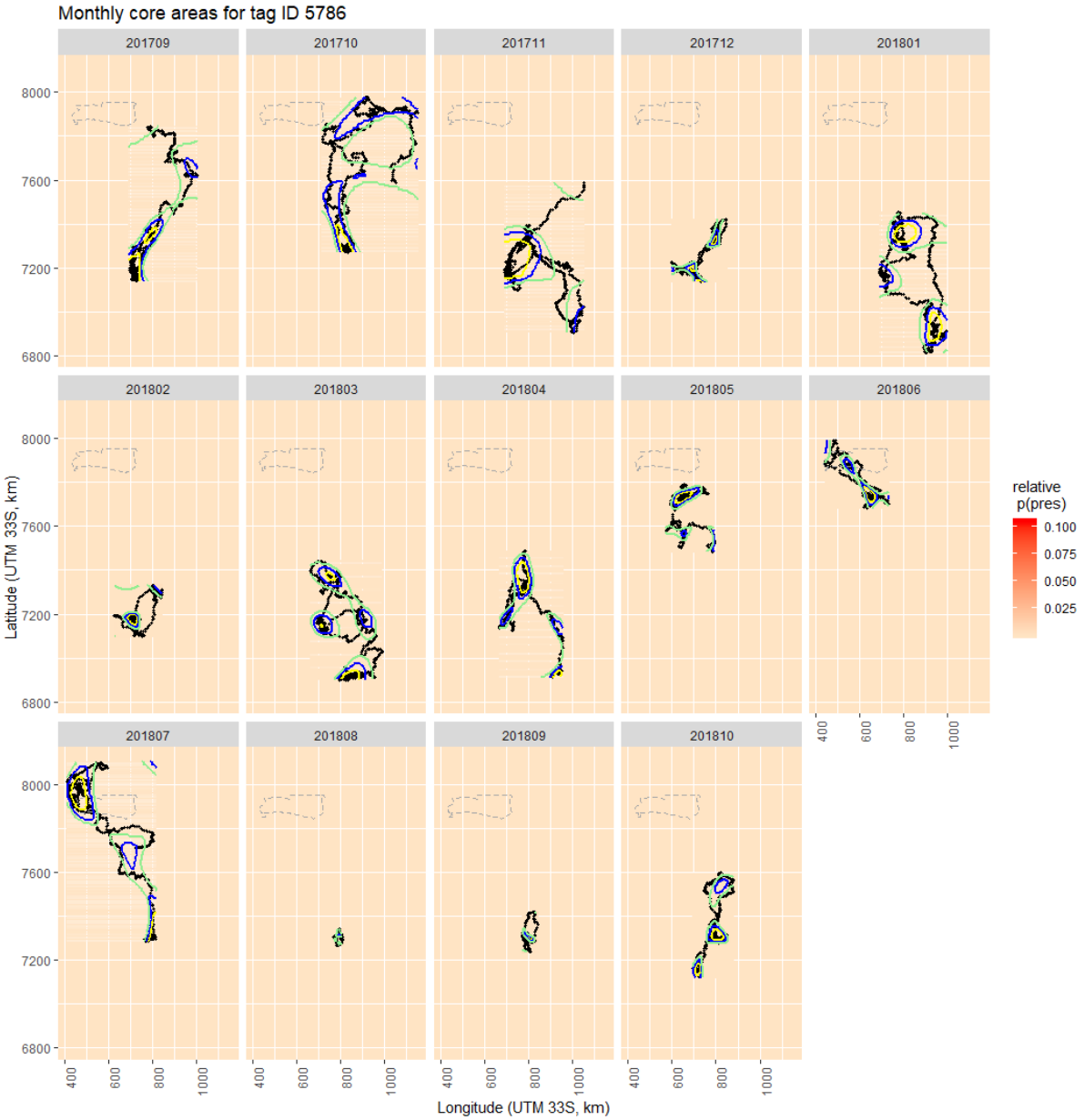


Figure 4-15 Variation in the mean monthly core area in terms of geographic location, shown with the relative probabilities of presence (in red gradient) and vulture locations (black dots). Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

The core areas for the months with tighter contraction and wider expansion for the two birds selected above were also contrasted. The *local* adult white-backed vulture (tag ID 5784) showed its largest monthly core area during December 2017 (3.10 th.sq.km [95%CI = 2.63; 3.73], taken from **Table V. 3** in the Appendix; **Figure 4-16**, top left) and its smallest during March 2018 (1.11 th.sq.km [95%CI = 0.85; 1.53]; **Figure 4-16,** top right). These areas of higher probability of presence concentrated in the central West part of Etosha NP. With regards to the *traveller* sub-adult white-backed vulture (tag ID

st2010-2700), the largest monthly core area took place during October 2017 (48.53 th.sq.km [95%CI = 36.90; 61.18], **Table V. 3** in the Appendix; **Figure 4-16**, bottom left); the tighter contraction during May 2018 (1.73 th.sq.km [95%CI = 1.28; 2.43]; **Figure 4-16**, bottom right). The largest mean core area expanded East-West at the South of Etosha NP, leaving out the vulture locations that extended farther North and Southwards. Additionally, in all but one (bottom left) map it is possible to see the core areas divided in two smaller non-contiguous parts at the central Northwest and South of Etosha, respectively.

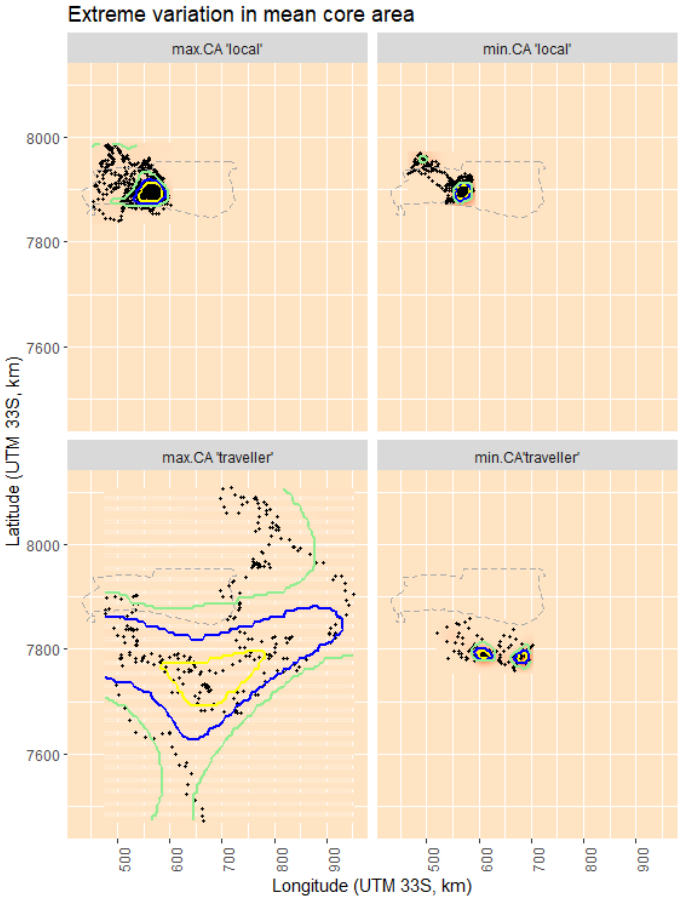


Figure 4-16 Variation in the mean core area in terms of geographic location, for four contrasting months, shown with the relative probabilities of presence (in red gradient) and vulture locations (black dots). Top: maximum (left) and minimum (right) expansion displayed by the *local* adult white-backed vulture tag ID 5784, which shows the smallest variation in the mean monthly home range. Bottom: maximum (left) and minimum (right) expansion performed by the *traveller* sub-adult white-backed vulture tag ID st2010-2700, with the largest variation in home range. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

Additional biological questions

Breeding and non-breeding adults, the *floaters*

The inspection of the changes in monthly range areas, both in temporal and geographical terms raised some interesting biological and ecological questions. Why did adult vultures have such distinct expansions and contractions in home ranges? There did not seem to be any clear temporal pattern, but would there be biological constraints to movement?

Two adult white-backed vultures were selected and their range areas inspected in more detail. The shape of their range areas during the reported time when this species lay their eggs in central Namibia (between April and June, [43]) were reviewed. The gender of the two birds is not known, but it is stated in the literature that white-backed vultures share the parental care [44]. Georeferenced locations were available between September 2017 and October 2018 for both birds. Also, both vultures utilised the same geographic area around Etosha NP. However, the two vultures showed differing movements. Maps of core areas are chosen to illustrate this point as they focus on the central areas of higher probability of bird presence.

The white-backed vulture tag ID 5786 travelled through the whole of Namibia (**Figure II. 6** in the Appendix) and only really restricted its movements to a smaller area during August 2018 (**Figure 4-17**). During this month it remained in an area South of Windhoek. Between April and June 2018 (highlighted with the yellow bars in **Figure 4-17**), vulture tag ID 5786 restricted somewhat its range areas but those still had large size and also showed very little overlap between months.

The white-backed vulture tag ID 5404, in turn, travelled mostly in the Northern part of Namibia and Southern Angola (**Figure II. 3** in the Appendix). It performed long trips and expanded significantly its monthly range areas, although not to the same extent as vulture tag ID 5786 (**Figure 4-18**). The two months with smaller core areas were March and April 2018 (408.20 sq.km [95% CI = 325.00; 525.00], and 684.30 sq.km [95% CI = 525.00; 875.00], respectively). This latter month fell within the time white backed vultures laid their eggs in central Namibia (highlighted with the yellow bars in **Figure 4-18**). The maps show a moderate size core area centred around the same locations, since November 2011; then compressing towards March 2018. In April the core area expanded progressively, and contracted once more later in the year. Moreover, looking also at early 2017 (top left maps in **Figure 4-18**), there was a remarkable expansion in the core area from May until July, then gradually compressing towards the end of the year.

What the monthly core areas might be displaying were expansion and contractions motivated by the breeding season. Might there have been incidental evidence to propose there were *floaters* (i.e., non-breeding adults) in the current study?

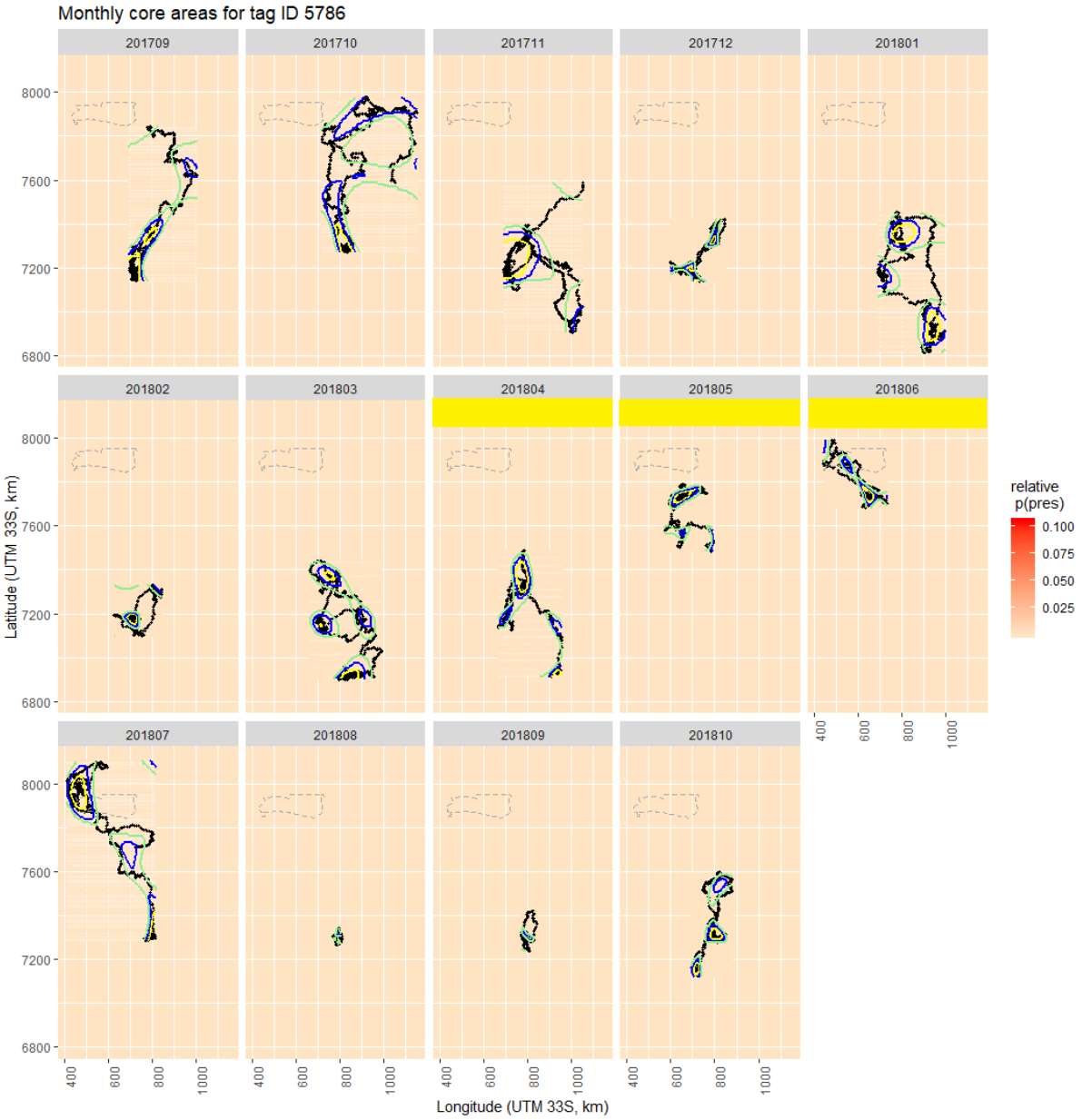


Figure 4-17 Illustration of the variation in the core area in terms of geographic location, highlighting the breeding season.

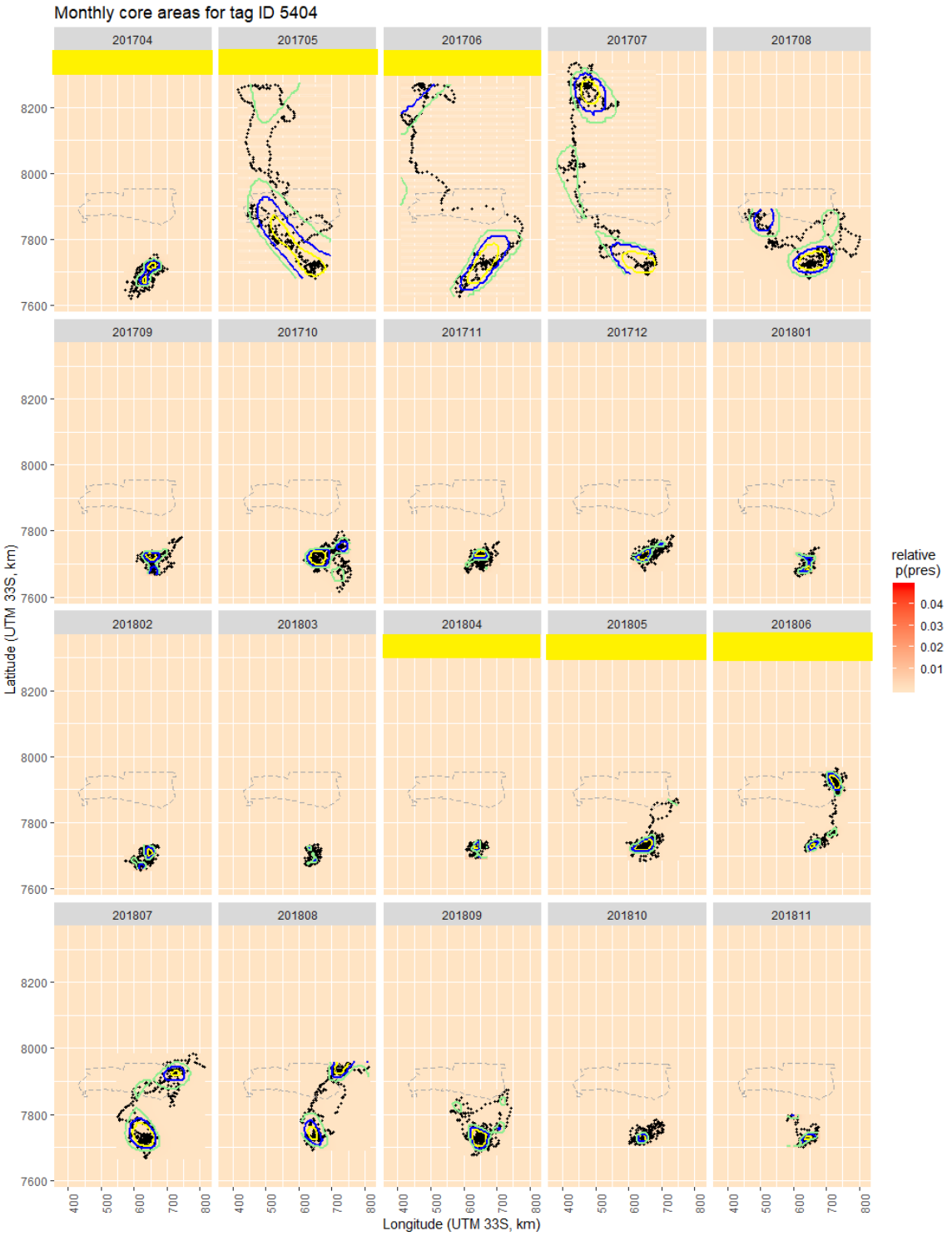


Figure 4-18 Illustration of the variation in the core area in terms of geographic location, highlighting the breeding season.

4.4 Discussion

Understandably, the level of detail made available in the literature depends on the aims of the study. Spiegel *et al.* presented one joint map of a kernel density estimate (KDE) for 14 white-backed vultures and five lappet-faced vultures (*Torgos tracheliotos*), tagged in Etosha National Park (NP) [73]. The maps presented in **Figure I. 2** and **Figure I. 3** show the birds used an extensive part of Namibia, with high intensity areas recorded south of Etosha NP all the way to the southeast of the country. There was also apparently high usage on the central-south areas of Etosha NP. No home range size was provided as the aims of the study related to smaller scale measurements of movement to describe flight mechanisms [73]. Bamford *et al.* briefly described the extend of movements by six Cape vultures and one white-backed that nested on the cliffs of the Waterberg Plateau (Namibia) [97]. Home ranges were determined using Minimum Convex Polygons (MCP) and areas varied throughout the year as a consequence of nesting behaviour (MCP were not mapped by the authors). Differences in areas were also recorded between age classes. The mean MCP for adults was 21,320 sq.km. whereas for the immatures (one of which was the white-backed individual) was 482,276 sq.km. The white-backed vulture "spent time in Etosha, and made an excursion into Angola" [97].

A third study described in greater detail the range areas of six immature white-backed vultures tracked in the North West Province of South Africa [39]. Phipps *et al.* compared the size of range areas using three different methods: 100% MCP, KDE (95% and 50% contours to represent the home range and core areas, respectively), and grid cell range (GCR). Each individual showed distinct sizes and shapes in their range areas which overall extended into six countries (**Figure I. 4**). Estimates varied greatly between methods and results from GCR are discussed as they were the most realistic and conservative representation of the movements. Monthly path GCR estimates varied between 600 and 22,200 sq.km. (mean ± SE = 9,878 ± 846 sq.km.; n=46 months) and showed their lowest at the beginning of the dry season [39].

With regards to the hooded vulture, four individuals tracked in northern Botswana showed smaller range areas during the dry (breeding) than in the wet (non-breeding) season [98]. Reading *et al.* present results for both methods implemented: 95% MCP and KDE (99%, 95% and 50%). For example, the mean 95% KDE ranged between 6,497.72 ± 2,267.78 sq.km. in the wet season and 1,329.15 ± 547.82 sq.km. in the dry season; the authors also alert for caution given the small sample size supporting those estimates (range areas were not mapped; [98]). Those data were analysed jointly with other studies from five other Southern African countries, even though results have not yet been made publicly available [92]. Regional variations in range areas were found, juveniles showed larger areas than adults, and males presented larger areas than females (irrespective of season).

Comparative studies have shown the various methods available to estimate range areas produce differing results, making the comparison between studies challenging [100, 105]. Failing to address the autocorrelation in the location data can also lead to estimates which are twice as small as they should be otherwise [100]. Even though only a small number of previous studies report estimates of range areas for the target species in this thesis, each implemented its own method, definition of season, and was supported by data collected at differing time intervals. As such, the discussion of movement pattern hereafter is made solely on relative terms, i.e. no numerical estimates are contrasted but rather the variations found (between age classes or seasons).

Size of monthly range areas

Grouping the vultures analysed per species showed the mean monthly home range and core area were at least 10 times larger for the white-backed than for the hooded vultures. This may not be surprising given the more gregarious behaviour displayed by hooded vultures [98]. The monthly mean home range size for white-backed vultures ranged between 1.17 thousand sq.km (th.sq.km) and 145.45 th.sq.km, while for hooded ranged between 0.37 and 4.46 th.sq.km. The respective mean core areas in turn, ranged from 0.25 to 48.53 th.sq.km, and from 0.05 to 2.00 th.sq.km. The two species showed overlapping 95% CI and additional care should be taken when interpreting these results as the number of individuals in each species varies greatly (15 white-backed and two hooded vultures). Despite the unbalanced representation of the two species, differences in range area sizes were expected. Hooded vultures are smaller birds and it has been suggested body size is positively related to range area size [115]. It has been pointed that for mammals such differences may be in part due to smaller energy requirements and a lesser ability to utilise low-quality forage [115]. This could also be the case to some extent in the case of obligate scavengers such as this study species. Despite the visible differences in range size between species, the ratio of core area to home range was surprisingly similar. Despite the marginally larger mean for the white-backed (0.25; 95% CI = 0.16, 0.33) than for the hooded vultures (0.23; 95% CI = 0.13, 0.39), the 95% confidence interval around those means overlapped greatly.

The size of monthly range areas per vulture were strikingly different. There was noticeable variability both between and within birds. The white-backed vultures showed varying levels of monthly range sizes with a good mix between age class. The sub-adult showed the larger range sizes while the two

immatures displayed little variation, although none was statistically different from the adults. The smallest (and narrowest) inter-quantile range area was recorded by the two hooded vultures.

Temporal variation

The variation in size of monthly range areas was also noticeable through time. Each vulture had distinct profiles but overall the majority of (individual) minima mean range areas occurred during the hot wet season (between January and May) while the maxima sizes occurred during the small rain season (between September and December). The individual variation in movement is also evidenced by the fact that some birds (up to 23.52%) showed synchronous minima and maxima, i.e., both extremes of its range area size were recorded during the same season. These findings agree with the temporal variation found in the mean daily movement properties (**Chapter 3**).

Displaying the sizes of home range and core area in the same plot further illustrated that even though core areas fluctuated through time, these fluctuations were less prominent. This was found for all vultures irrespective of species. The hooded vultures had smaller range areas but with no statistical differentiation, i.e., there were overlapping 95% CI between these and some white-backed vultures.

The ratio between the core area and home range size is very interesting but not so easy to interpret. Numerically, the same values can be generated from different combinations of home range and core area sizes and this is somehow expressed in the similar average found between all birds in this study, despite the striking differences in range areas. Only on two occasions did birds show a monthly mean ratio larger than 0.52 (tag ID 5403 in March 2018, 0.52 [95% CI = 0.20; 1.00]; and tag ID st2010-1330 in September 2015, 0.53 [95% CI = 0.52; 1.00]). Despite the uncertainty around those means, this suggests only very seldom did vultures explore their territory in a homogeneous way (signalled by a ratio of 0.56, per definition). On 79.58 % of months, the ratio of core area to home range size fell between 0.20 and 0.33, irrespective of species or age class. This indicates vultures explored home range areas three to five times larger than their core area. Additionally, even comparing the monthly mean ratio from the vulture that showed the smallest variation in the mean monthly home range (the *local* adult white-backed vulture tag ID 5784), with the vulture that showed the largest variation (the *traveller* sub-adult white-backed vulture tag ID st2010-2700), we found overlapping results.

These findings suggest vultures are very adaptable in how they use their environment. Each bird seemed to show its own temporal variation of range size, with no clear separation found between age group, *local* vs. *traveller* or age class. These points were only briefly illustrated and targeted statistical

tests would be necessary to make sound conclusions. Nonetheless it may be that, in terms of ecological meaning, each vulture keeps a core area of preferential size, perhaps dictated by body size, animal fitness and/ or the likelihood of finding shelter and key resources [79]. The level of expansion in monthly home range may have been due to the environmental quality of the geographical area, or breeding status. If an animal found an area with adequate food and water, then it may not need to explore far larger home ranges. On the other hand, the lack of pattern in the temporal variation of range areas, and the unpredictable availability of prey for African vultures [12] may well explain why in some months these birds have to expand their home ranges up to five times the size of their core area. Each individual personality [70] may also play an important role in explaining the variations found in range sizes, with each bird moving according to its cognitive map [79]. The reproductive status is also known to dictate the movements of African vultures [97] even though that information is not available for the adults monitored in this thesis. Observational studies would be necessary to ground truth these suggestions.

Spatial variation

The variation in the monthly range areas was noticeable also in terms of shape as well as geographic extent. We found marked expansion and contraction of the areas with higher probability of presence of vultures through time. Birds were capable of changing the extension of the area they use each month, sometimes with little or no overlap visible between consecutive months. Each bird again, showed its own variation, even showing differences between years.

Taking the example of the adult white-backed tag ID 5786 – it showed striking changes in the spatial extent of the range areas from month to month, often the mean core area included non-contiguous areas (i.e., it was formed by smaller areas that did not touch), August 2018 showed an outstanding contraction of range areas, and the spatial extent recorded during September and October 2017 were very different in shape with only a small geographical overlap. During August 2018, the bird stayed very local around an area South of Windhoek where there are tourism and commercial farms. It is known there are occasional discards of goat skins from those farms. There are also *Acacia* trees in the area, making this location an advantageous place to be with a good provision of food and shelter (G. Shatumbu, *pers. comm.*). This reinforces the suggestion put forward that vultures will not need to expand their range areas when they locate an area of high resource availability.

Kendall *et al.* highlighted the importance of prey abundance as well as prey mortality, and how their spatial and temporal patchy occurrence can shape the movement of vultures between seasons [96].

They followed migratory Western white-bearded wildebeest (*Connochaetes taurinus*) across an area of known distinct and asynchronous rainfall gradient and showed vultures gathered round the herds during the dry season, when herds experience their highest mortality. Further they described that white-backed vultures preferred wetter areas during the wet season. Vultures in Etosha NP also follow closely the outbreaks of anthrax. Most cases of anthrax in Etosha NP occur in the wet season [116].

Another interesting consideration is that of birds returning to places visited previously. Birds showed repeated visits to particular geographic areas, at varying distances in time. The adult white-backed vulture tag ID st2010-2608 for example, moved slightly differently in each month but always kept a core area in the central part of Etosha National Park. On the other hand, the sub-adult and another adult performed long circular trips, returning to previously visited territory in Etosha months later. This movement behaviour could once more be explained by the link between home range and the cognitive map of an animal [79, 111]. Those concepts merge suggesting an animal retains knowledge about places that have some value, such as food resources, travel routes, or locations where members of the other sex were seen [111].

Furthermore, monthly range areas overlapped with protected areas all throughout the year, for all but one vulture (tag ID 5789; see all range area maps in **Appendix VI**). Even though only Etosha and Bwabwata NPs were represented (showing the areas where tag deployments took place) it sufficed to demonstrate the importance of protected areas in habitat use. The usage of protected areas by vultures has been documented [10, 39] and these areas are particular important for instances for the safeguard of nests (e.g., [117, 118]).

Breeding and non-breeding adults, the *floaters*

It is known immature birds have the ability to explore larger areas than adults [39]. The sub-adult examined in this thesis followed that pattern even though the two immatures stayed fairly local, and three adults performed large trips. But it could be that individuals of any age class show larger movements moving in a nomadic manner from one food source to another, avoiding competition with conspecifics for the same food supply [5, 39]. Additionally, it has been suggested some adults may travel farther when no suitable nesting habitat is available [11], the so called “floaters”. Floaters are present in many bird populations as the breeding season separates out the territorial breeding birds from the non-territorial, usually non-breeding, floaters [11, 119].

Two of the adult white-backed that explored large geographic ranges were contrasted and their movements inspected with special attention put on the breeding months. This species is known to lay eggs mostly between April and June [43]. While one adult roamed freely with no apparent change around that time, the other (tag ID 5404) did show a large variation in its range areas. One interpretation on the movements from this bird could be as follows- as April approaches (or as early as March for the vultures measured in Etosha [43]), breeding pairs need to build or restore their nest, needing to spend a good proportion of their time around that elected location; birds would compress gradually their core areas with the minimum achieved during the month the egg was laid; once the egg hatches, the breeding pair sets out to meet the higher energetic demands, expanding once again the range areas significantly. The adult tag ID 5404 spent April 2018 in an area not far from the abattoir SW of Otjiwarongo. There are also private game farms in the vicinity, with large animals such as rhino and giraffe. Additionally, there is a small river and big trees that could be used to build a nest (G. Shatumbu, *pers. comm.*).

There was incidental evidence to suggest that the white-backed vulture tag ID 5786 was a non-breeding adult, a floater, exploring freely its geographic range at any time of the year. Furthermore, there is some indication that the white-backed vulture tag ID 5404 was a breeding adult, shaping its movements according to breeding demands. Nevertheless, in order to know with certainty, the breeding status of these (and the remaining) vultures, it would be necessary to analyse in more detail the data recorded by the transmitters and/ or conduct field observations.

To conclude, estimates of monthly range areas were presented, with associated measure of uncertainty. Estimates were described for home ranges and core areas, separately as well as a ratio to further detail the movement patterns of the study species. Monthly range areas varied in size, shape and geographic location. Differences were perceived both within and between birds. Range sizes were generally smaller for the hooded vultures, but with differences detected over time nonetheless.

The size of monthly range areas per vulture were strikingly different, in particular those of home ranges. Interestingly, core areas also varied but within a narrower range of values, suggesting birds may keep areas with higher usage of a suitable size, then expand their wider usage area according to the energetic or reproductive needs. Also, the ratio of core area to home range showed very little

variation even when contrasting birds with strikingly differing range area sizes, showing vultures display a consistently patchy use of their environment.

Differences between adults and immatures were not as clearcut as one would expect from the literature. Speculation was made about the biological and ecological implications, and it may be that the population of white-backed vultures in the study area has non-territorial non-breeding adults, the *floaters*. Additionally, the individual variations seen in the monthly movement characteristics supported the importance of internal factors such as personality and the concept of cognitive maps in tailoring the choices of movement by each bird.

The method implemented throughout this thesis adequately captured the autocorrelation structure of the geo-referenced locations analysed. This precluded numerical comparison with previous studies but we expect this represents a more faithful habitat usage of the vultures monitored. Previous estimates of range areas may be under-representing the areas utilised by animals, which may have detrimental consequences for species conservation. It is crucial that management and mitigation actions cover the entirety of the areas of higher importance for the target species. Moreover, it was shown that the range areas intersected protected areas and this is investigated further in **Chapter 5** with the inclusion of environmental covariates.

5 Habitat modelling

This chapter focuses on the characterisation of the monthly areas of preferential usage identified for each vulture. Nine environmental covariates are assessed; those describe habitat characteristics, climate variables, and human presence. The habitat preferences are modelled for each vulture individually, incorporating also a temporal (bird-month) and a spatial (geographic coordinates) term. The relationships found between covariates and vultures are discussed and individual patterns are contrasted. Special emphasis is given to the importance of protected areas and support is provided for transnational conservation initiatives. Lastly, predictions are mapped showing the seasonal distribution for each bird.

Note: It is anticipated that the findings from the habitat modelling will be published in a high impact animal conservation journal to reinforce the link between science and conservation, and expand on the applications this study can have in the preservation of endangered wildlife species.

5.1 Introduction

Animal movement has long been the centre of research in ecology [3]. This is in part owed to the link that movement of individuals can establish between the individual and the population, both in spatial and temporal scales [120]. Inspecting the patterns of individual movement has enhanced the understanding of spatial dynamics at also increasingly levels of ecological structures (from patches to meta-communities) [121]. At the same time, landscape ecologists have concentrated on the interaction between individuals and their environment, motivated by the causes and consequences of impacts from habitat loss and climate change on the organisms [121].

The environmental characterization of animal movement tracks has allowed researchers to address crucial aspects of movement ecology and conservation. Researchers have identified critical habitat patches, assessed the impacts of fragmentation or obstacles to movement patterns, described connectivity movements and wildlife corridors; models have been built to explain resource use and the habitat suitability for conservation and reintroduction measures (see [3] for a review).

The growing developments in satellite-based technology have enabled access to increasingly detailed information on animal movement and their environment [3]. Remote sensing (or the modelled products from remote sensing) provides a characterisation of the environment in which animals move and the complex interactions between movement and environment can be evaluated using powerful modelling frameworks [1].

Information about the environment can be gathered *in situ* (e.g., weather stations on the ground) but remote sensing is key in studies of highly mobile species, over large or remote areas. There are growing amounts of environmental data being made publicly available, but these come in heterogeneous sources, formats and resolutions [122]. Of great benefit to researchers, advances are also being made in the development of systems that bridge the two aspects (i.e., the volume and specifications of the data), one such being the Environmental-Data Automated Track Annotation (Env-DATA). This system automates the annotation of geo-referenced animal locations with external factors from their surroundings such as weather, habitat types, and human land use [122].

Indices derived from remote-sensing data such as the Normalized Difference Vegetation Index (NDVI) have been used extensively. The NDVI variable provides a good approximation of vegetation density and is frequently used as an index of primary productivity. Is has been included in studies across taxa and proven valuable in predicting the distribution, abundance, and life history of organisms (see [123] for a review). Local primary productivity influences the entire food web and NDVI has also been linked to vulture movement. Turkey vultures (*Cathartes aura*) in America reduced their home ranges at times of high productivity, when the need to forage for food was lower [122]. With improved access to weather information, the number of studies that integrate such information is also increasing [3]. Movement decisions of migratory birds have been linked to meteorological conditions such as wind and barometric pressure, for species as varied as European bee-eaters (*Merops apiaster*) [124] and turkey vulture [125]. Temperature and altitude-specific wind conditions have been useful to determine energetic costs, physiological constraints on flight, and to identify the importance of thermal or orographic (i.e., related to the topographic relief of mountains) uplift in flight behaviour [126].

The combined analysis of movement tracks with environmental covariates allows evaluation of how habitat elements or resources are used at distinct time scales (e.g., sequentially, daily or seasonally), age classes or biological stages, and for explicit behaviours and purposes [127]. Despite extensive work, the patterns over time of animal movement through variable landscape are not yet fully understood [128]. Resource availability can be seasonal and/ or show variation between years, and

internal resource demands also change throughout the life-history of the organism [128, 129]. Moreover, the availability of resources at a point in time reflects from cumulative outcomes of natural elements (e.g., rainfall, fire, grazing) that define the resource availability along previous time scales (e.g., days, or months) [130]. The long term-patterns that animals exhibit through the environment arise from their repeated movements, as the animal gathers information about the landscape as it moves towards/ from a selected resource [128]. This can be reflected on movement metrics such as tortuosity and speed, which vary according to behaviour and resource acquisition (e.g. [131, 132]). When crossing a less favourable environment individuals will move faster; conversely, individuals will tend to linger in safer areas with richer resources [133]. Also, animals will move away from unwanted stimuli such as predators or other dangers, as well as human disturbance [134].

The assessment of habitat preferences provides a measure of the relationships between a species and its environment [135, 136]. Knowing where animals are, what characteristics of the environment tailor their choice of habitat and how this choice changes with time are critical in understanding the ecology of species [135]. Habitat preferences are also critical in identifying areas of high importance, assessing human-wildlife overlaps, and more so, guiding appropriate conservation efforts [135]. Conservation programmes are often targeted at high-profile and/or umbrella species such as top predators [137]. Raptors can also be seen as such priority and iconic species and some studies have focused in describing their habitat associations [137]. Raptors often occur over large areas encompassing many habitat types. Nonetheless, studies have often focused on a relatively small geographic scale (such as Cape vulture (*Gyps coprotheres*) and other species in Lesotho [138], or Bonelli's eagles (*Hieraaetus fasciatus*) in the South of Spain [139]); studies also often focused on particular aspects of the biology of these species such as nesting (e.g., [137]).

This chapter integrates environmental data with geo-referenced animal locations. It puts the movement ecology of the study species in the context of their surroundings by making a characterisation of the habitat each vulture utilised. The aims were to:

i) define and characterise the study area where all vulture locations were recorded, based on environmental covariates (habitat characteristics, climate variables, and human presence);

ii) model the habitat preferences for each vulture individually, incorporating also a temporal (bird-month) and a spatial term (geographic coordinates);

iii) describe the importance of the environmental covariates for each vulture, with special relevance on the biology and conservation of the species.

In particular, this chapter also investigated how individual vultures may employ different strategies in exploring the surrounding environment.

5.2 Methods

5.2.1 Data specifications

The data analysed in this chapter consisted of 238,499 geo-referenced locations from 16 vultures, recorded between March 2015 and November 2018. Fourteen white-backed vultures (11 adults, one sub-adult and two immatures), and two hooded vulture (one adult and one immature) were included (**Table 5-1**). Vulture tag ID 5215 was excluded from analysis due to the shortage of information for this bird (the tag only transmitted for three months). All other vultures were monitored for five to 35 months, each month containing data of 10 or more days. The number of geo-referenced locations per bird ranged from 3,697 (tag ID st2010-2608) to 34,843 (tag ID 5785).

Table 5-1 Details of the 16 vultures examined in the study of habitat preferences. The transmitter identification (Tag ID) is shown as well as the start and end date of recorded locations included in the analysis, total number of locations per bird, and number of months monitored with respective mean number of monthly data points (range shown in brackets). Deployment area (NP = National Park). Species and age class as: adt. – adult, wbv. - white-backed vulture, hv. – hooded vulture. Also, white-backed vultures shown in black, and adult hooded vultures highlighted in blue; sub-adult and immature highlighted in bold.

Tag ID	Start analysis	End analysis	no. locations	Months monitored	no. per month mean (range)	Deployment area	Species and age class
5403	2017-05-01	2018-03-31	14,090	11	7,684.45 (4,632-8,958)	Etosha NP	adt. wbv
5404	2017-04-01	2018-11-11	26,921	20	8,075.7 (3,264-9,654)	Kunene Region	adt. wbv
5784	2017-08-01	2018-03-30	17,514	8	13,130.5 (11,712-14,297)	Etosha NP	adt. wbv
5785	2017-08-01	2018-11-11	34,843	16	13,058.62 (4,932-14,308)	Etosha NP	**imm. wbv**
5786	2017-09-01	2018-10-23	31,484	14	13,460.93 (10,398-14,447)	Etosha NP	adt. wbv
5787	2017-11-01	2018-11-10	23,309	13	10,772.77 (4,374-14,411)	Bwabwata NP	adt. wbv
5788	2017-11-03	2018-11-11	15,397	11	8,393.45 (2,430-13,194)	Etosha NP	adt. wbv
5789	2017-11-01	2018-03-16	8,163	5	9,790.4 (5,622-11,364)	Bwabwata NP	adt. wbv
CAT1	2017-11-01	2018-11-11	24,347	13	11,210.85 (4,344-12,249)	Bwabwata NP	**imm. hv**
st2010-1330	2015-03-01	2016-04-11	4,416	14	1,890.64 (720-2,046)	Bwabwata NP	adt. hv
st2010-1332	2015-03-01	2018-04-10	8,784	35	1,501.37 (618-1,914)	Bwabwata NP	adt. wbv
st2010-2607	2017-03-01	2018-11-11	4,978	21	1,422.05 (540-1,500)	Etosha NP	adt. wbv
st2010-2608	2017-04-01	2018-11-11	3,697	17	1,304.71 (528-1,504)	Etosha NP	adt. wbv
st2010-2609	2017-06-01	2018-04-26	3,786	11	2,066.09 (738-4,278)	Etosha NP	adt. wbv
st2010-2697	2017-05-01	2018-07-26	7,684	15	3,072.8 (2,124-4,272)	Etosha NP	**imm. wbv**
st2010-2700	2017-06-01	2018-11-11	9,086	18	3,024.83 (1,056-3,840)	Etosha NP	**s_adt. wbv**

5.2.2 Environmental covariates

Nine environmental covariates were gathered to investigate the habitat preferences of each vulture in this study. The environmental covariates fell into three categories: 1) habitat characteristics: type of land cover, vegetation index, distance to nearest river, and elevation; 2) climate variables: temperature and precipitation; and 3) human presence: inside or out of a protected area, population density, and distance to nearest road (see details in **Table 5-2**; and **Figure VII. 1** to **Figure VII. 9** in the Appendix, see also for further description of land cover and protected areas).

Table 5-2 Description and source of the nine environmental covariates investigated. Spatial and temporal resolution shown, as well as units. List of acronyms (in order of appearance): MODIS- Moderate Resolution Imaging Spectroradiometer; NDVI- Normalised Difference Vegetation Index; EIS- Environmental Information Service Namibia; OSM- OpenStreetMap; ASTER- The Advanced Spaceborne Thermal Emission and Reflection Radiometer; DEM- Digital Elevation Model; ECMWF- European Centre for Medium-Range Weather Forecasts; WDPA- World Commission on Protected areas; ESRI- Environmental Systems Research Institute.

Covariate	Description and source	Spatial resolution	Temporal resolution	Units
Habitat characteristics				
Land cover	GlobCover > Land Cover 2009 Source: Movebank at https://www.movebank.org/	300-m	8-days (2004 to 2009)	(no units)
Vegetation index	MODIS Land > Vegetation Indices 1-km Monthly Terra (MOD13A3 V6) > NDVI Source: Movebank at https://www.movebank.org/	1-km	month	(no units)
Distance to nearest river	Perennial rivers that intersect the study area Sources: EIS at http://www.the-eis.com/ and OSM at http://download.geofabrik.de/	N/A	N/A	m
Elevation	ASTER ASTGM2 Global 30-m DEM Source: Movebank at https://www.movebank.org/	1 arc-second	N/A	m
Climate variables				
Temperature	MODIS Land > Land surface temperature & Emissivity 0.05-deg Monthly Terra (MOD11C3) > Land Surf Temp Day Source: Movebank at https://www.movebank.org/	0.05-deg	month	Celcius
Precipitation	ECMWF > Interim Full Daily at Surface Forecast > Total Precipitation Source: Movebank at https://www.movebank.org/	0.75-deg	3-hourly	m
Human presence				
Inside or out of protected areas	World Commission on Protected Areas source: WDPA at https://protectedplanet.net/	N/A	N/A	N/A
Population density	Global Rural-Urban Mapping Project (GRUMP) v1 > GRUMP 2000 Population Density Adjusted Source: Movebank at https://www.movebank.org/	30 arc-second	5-yearly (2000)	persons/sq.km
Distance to nearest road	Main roads that intersect the study area Sources: OSM at http://download.geofabrik.de/ and ESRI at https://www.arcgis.com/	N/A	N/A	m

Six of the environmental covariates were sourced from Movebank [122]. Data were extracted using both the geographic coordinates and the time stamp from each vulture data point (for e.g., 21-04-2017 16:15:06). Data were also extracted at the best available spatial and temporal resolution, from the suite of products available on Movebank. The spatial resolution ranged from 30 meters (elevation) to 0.75 degrees (equivalent to app. 83 km at the latitude of Namibia; precipitation). The temporal resolution ranged from 3-hourly (precipitation) to 5-yearly (population density). Nonetheless, habitat information was missing for some data points; vegetation index, temperature and population density were not available for the entire dataset. Those data points represented 0.26% of the data set and were removed. Not all classes of land cover were represented in the data; classes with less than five vulture locations in a month were merged into one other class called "1234". The range of values for population density was very wide (up to 17,471 persons/sq.km) even though only 0.76% of the study area had more than 100 pers./sq.km (see below for definition of the study area). Therefore, three population density classes were created based on quantiles, as follows: "POP.1" up to 0.2693 pers./sq.km, "POP.2" from then to 1.5911 pers./sq.km, and "POP.3" with more than 1.5911 pers./sq.km. Additionally, the units from two covariates were converted into more intuitive units; temperature was changed from Kelvin to Celsius degrees and precipitation from meters to millimeters (as mean values were extremely low). The vegetation index was characterised by the Normalised Difference Vegetation Index (NDVI). NDVI is a measure of how green the vegetation is, calculated from the visible and near-infrared light reflected by vegetation (https://earthobservatory.nasa.gov/). The index ranges from -1 to +1; a zero means no vegetation and close to +1 (0.8 - 0.9) represents the highest possible density of green leaves.

The remaining three environmental covariates (inside or out of protected areas, distance to nearest river or distance to nearest road) were generated in R version 3.6.0 [62], with RStudio v. 1.1.456 [85]. The areas with conservation status were collected via the World Commission on Protected Areas website (WDPA, https://www.protectedplanet.net/). All the protected areas were considered, irrespective of size or the level of conservation applied. Vulture locations were determined to be inside or outside one of those protected areas using the sf package in R [140]. With regard to rivers, only the main course of the perennial rivers that intersected the study area were considered. The geographic contour of those rivers were collected from the Environmental Information Service Namibia (EIS, http://www.the-eis.com/) and OpenStreetMap (OSM, https://www.openstreetmap.org) and manipulated in R. Thirdly, only the main roads in each country that intersected the study area were considered; those features were gathered from OSM and Environmental Systems Research Institute (ESRI) and merged in R. Distances from each vulture location to the nearest river or road were

calculated using the rgeos package [141]. The majority of the exploratory plotting was done with the tmaptools [142] and tmap [143] packages.

5.2.3 Study area

The study area was defined as the minimum bounding rectangle (MBR) within which all vulture locations occurred. The rectangles were oriented in a North-South and East-West direction, and the area overlapping with the sea, on the West, was excluded (**Figure 5-1**). An additional buffer of 1 km around the MBR was created in order to better include the locations that fell in the borders of the study area. Overall, vulture locations spanned over the majority of Namibia (where tag deployment took place) and parts of its five neighbouring countries as well as Lesotho.

The resulting study area encompassed 2,347,173 sq.km, extending through a maximum of 1,705 km in northing (latitude) and a maximum of 1,495 km in easting (longitude). For comparison: the area of Namibia represents 35.17% of the study area, the area of the United Kingdom is 10.33% of the study area, and the area of Portugal is 3.92% of the study area.

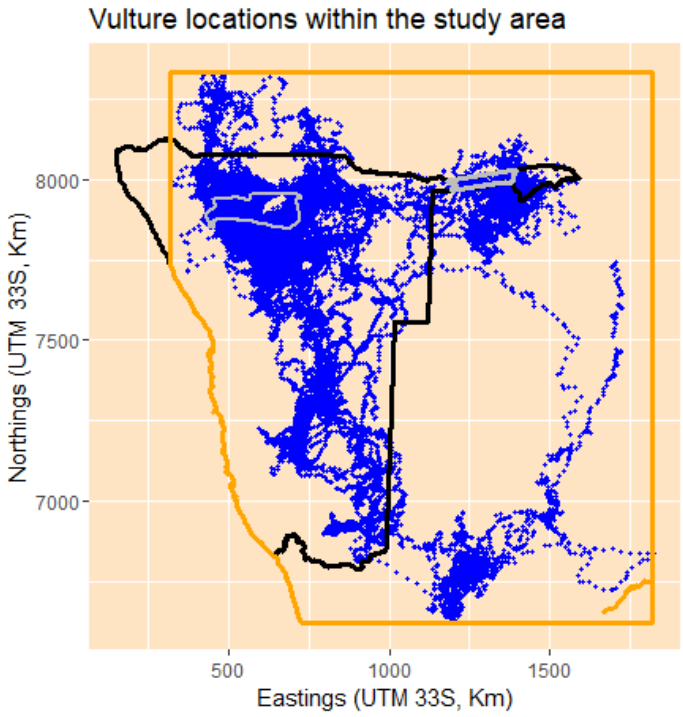


Figure 5-1 Boundaries of the study area (orange) encompassing all the vulture locations (blue). The borders of Namibia (black) and of both Etosha and Bwabwata National Parks (grey) are shown for reference. The border of Lesotho intersecting the study area on the South-eastern corner is also shown (orange).

The characterisation of the study area was based on the environmental covariates described earlier (**Table 5-2**). The study area was divided into 5 km x 5 km grid and each grid central point was used to extract the six covariates sourced from Movebank [122]. Elevation, population density and land cover (i.e., the type of land use or existing vegetation) were considered static variables as they were not expected to change between the start and end date of the recorded locations included in the analysis. These were extracted once, using the geographic coordinates of the study area grid. Vegetation index, land temperature and precipitation were dynamic variables as they change throughout the year. These data were extracted three times, once for each month representative of each season considered in the present study. An initial assessment showed the following months represent well the respective seasons: March for the hot wet season, July for cold dry, and November for small rain. Furthermore, the bird locations analysed here spanned from 2015 to 2018 and it was not viable within the time frame for this study, to gather all information for all 12 representative months. As such, 2017 was taken as the example year. Data was extracted for the first day of each of those months, at mid-day (i.e., 01-03-2017 12:00:00, 01-07-2017 12:00:00, and 01-11-2017 12:00:00).

Table 5-3 shows the range of values found within the study area for each environmental covariate considered.

Table 5-3 Characterisation of the study area with respect to the environmental covariates investigated. The range of values (with mean value inside brackets) is shown for the continuous variables; values represent averages per grid cell. Values are also shown per season when applicable.

Covariate	Units	Range of values per 25 sq.km grid cell (mean)
Habitat characteristics		
Land cover	(no units)	14 categories (see **Appendix VIII** for description)
Vegetation index	(no units)	Mar: -0.18 - 0.89 (0.47); Jul: -0.19 - 0.75 (0.31); Nov: -0.18 - 0.75 (0.26)
Distance to nearest river	m	0.40 - 616,261.80 (168,681.80)
Elevation	m	0.00 - 3,092.80 (1,103.90)
Climate variables		
Temperature	Celcius	Mar: 20.18 - 53.81 (31.87); Jul:11.26 - 37.61 (25.35); Nov: 22.69 - 54.66 (41.36)
Precipitation	mm	Mar: 0.00 - 12.04 (2.50); Jul: 0.00 - 3.22 (0.04); Nov: 0.00 - 8.71 (0.60)
Human presence		
In/ out of protected areas	N/A	inside: 25.90%; outside: 74.10%
Population density	persons/sq.km	0.00 - 17,471.12 (8.22)
Distance to nearest road	m	0.10 - 376,268.80 (70,348.70)

Fourteen land cover categories were present in the study area (**Table 5-3**, see **Figure VII. 1** in the Appendix with full description of each class). “Closed to open (>15%) grassland” (class “140”) was present in 57.31% of the study area. This was followed by “mosaic vegetation (grassland, shrubland, forest) (50-70%) or cropland (20-50%)” (class “30”), present in 11.57%, and “open (15-40%) broadleaved deciduous forest (>5m)” (class “60”), present in 7.72% of the study area. Furthermore, “water bodies” represented 0.45% and “artificial surfaces and associated areas (urban areas >50%)” 0.14% of the study area. The vegetation index (characterised by the Normalised Difference Vegetation Index, NDVI), changed noticeably across the study area throughout the selected months (March, July and November 2017; **Table 5-3** and **Figure VII. 2** in the Appendix). March showed the highest variation with a mean of 0.47 with the lower values congregated in the western and mostly southern section of the study area. Those lower values extend throughout the study area along the year with November showing a patchier geographical pattern. There were a small number of negative values (1.07%) all throughout the year highlighting areas of water and the salt pan in Etosha National Park. For context, moderate values of NDVI from 0.2 to 0.3 represent shrub and grassland (https://earthobservatory.nasa.gov/).

Seven perennial rivers overlapped the study area (**Figure VII. 3** in the Appendix). These rivers took distinct names in different countries or regions. Their names and the countries they intersect were: 1. Cunene (Angola), Kunene (Namibia); 2. Cubango (Angola), Okavango (Namibia, Botswana); 3. Cuito (Angola), and Khwai river (Botswana); 4. Cuando (Angola), Chobe and Linyanti (Namibia), Kwando (Botswana); 5. Zambezi (Namibia, Zimbabwe, Zambia, and Botswana); 6. Limpopo (Zimbabwe, Botswana); and 7. Orange (Namibia, South Africa also with Vaal river). The mean distance from any grid cell central point to the nearest river was 168.68 km, ranging to a maximum of 616.26 km (**Table 5-3**).

The topography in the study area was patchy with elevation sitting mostly below 1,200 m (**Table 5-3** and **Figure VII. 4** in the Appendix). The highest elevation was found on the SE region with the mountain range of Lesotho peaking just over 3,000 m.

Land temperatures were quite variable across the selected months (taken from mid-day of the first day of March, July and November 2017) as well as across space throughout the study area (**Table 5-3** and **Figure VII. 5** in the Appendix). The minimum average record per (25 sq.km) grid cell was recorded in July (11.26 °C) when temperatures varied less and were only warmer in the Western border of the study area. Average temperatures in a grid cell were higher than 50 °C during the other two months, and the study area was quite homogeneous in November with only 1.03% of the area recording temperature below 35 °C (SE corner).

The total precipitation also changed distinctly across the study area and throughout the year (**Table 5-3** and **Figure VII. 6** in the Appendix). Overall, the average records per (25 sq.km) grid cell taken at the selected times ranged from 0.00 to 8.71 mm. 76.53% of records related to an average precipitation less than 1 mm (from all seasons), and only 1.07% of the records represented average precipitation greater than 10 mm (during the hot wet season). In fact, most of Namibia has been experiencing records below normal rainfall since 2013 [52]. President Hage Geingob has recently declared a state of emergency due to the current drought; this was the third time in six years that the government has declared such emergency [52].

The study area included over 1,000 protected areas with sizes up to 64,362.55 sq.km (**Figure VII. 7** in the Appendix). In particular, Etosha National Park (NP) has 22,270 sq.km and Bwabwata NP has 6,274 sq.km, together representing 1.22% of the overall study area. All areas were designated terrestrial protected areas but their characteristics were diverse (see **Table VII. 1** to **Table VII. 3** for description of each class). Namely, there were distinct International Union for Conservation of Nature (IUCN) management categories, governance or ownership types. For the purpose of this analysis all areas

were considered equally important and 25.90% of the grid cells contained an area with some level of protection (**Table 5-3**).

The human population density was generally low within the study area (**Table 5-3**, and **Figure VII. 8** in the Appendix). There were on average 8.22 up to a maximum of 17,471.12 persons/ sq.km (around Johannesburg, South Africa). Nonetheless, only 0.76% of the study area contained more than an average of 100 persons/ sq.km.

Several roads intersected the study area. However, for the purpose of this analysis, only the main ones were considered (**Figure VII. 9** in the Appendix). A total of 43 roads were included and their designations were: EN- roads in Angola (100, 110, 120, 140, 160, 170, 180, 280, 295), M10 in Zambia, A8 in Zimbabwe, A- roads in Botswana (1 to 3) and in Lesotho (1 to 5), N-roads in South Africa (1 to 18) and B- roads in Namibia (1 to 8, except 5 and 7). The mean distance from any grid cell central point to the nearest road was 70.35 km, ranging to a maximum of 376.27 km (**Table 5-3**).

5.2.4 Habitat modelling

Model structure

One model was fitted for each bird separately. The probability of presence of each vulture throughout the study area was modelled as a function of covariates using Bernoulli Generalised Additive Models (GAMs; [21, 54]), it employed a spatially adaptive smoother using the CReSS approach and permitted autocorrelated residuals. Pseudo-absence locations were randomly generated from within the respective available area. The available areas were defined as the minimum bounding rectangle (MBR) within which the locations for a vulture occurred, in a given month; there were as many MBR as "bird-month". For each vulture location (presence), five pseudo-absences are drawn (refer to **Section 2.4** for further explanation). Some vulture locations on the West of the study area overlapped with sea. As per the definition of the study area, all those points over the sea were removed.

Eleven explanatory variables were used to model the probability of presence of each vulture. These were the nine environmental covariates (land cover, vegetation index, distance to nearest river, elevation, temperature, precipitation, inside or out of protected areas, population density, and distance to nearest road), the geographical coordinates (projected to UTM 33 S, easting and northing, in meters, herein referred to the "spatial term"), and time (i.e., each year-month combination, herein referred to as the "temporal term"). Each variable was included in a model either as categorical or continuous. To each continuous variable, a spatially adaptive smooth function was applied; quadratic

B-splines are used. A spatial term was included as a bivariate smooth using a CReSS smoother. The spatial term was also included in the model as an interaction with the temporal term to allow the probability of bird presence to change both spatially and temporally.

The initial model for each bird included all explanatory variables:

$$g(E[Y_{it}]) = \beta_0 + \boldsymbol{\beta}_{land\ cover} + \beta_{prot.\ area} + \boldsymbol{\beta}_{pop.\ density} + f(x_{veg.\ index\ it}) +$$

$$+ f(x_{dist.\ river\ it}) + f(x_{elev.\ it}) + f(x_{temp.\ it}) + f(x_{precip.\ it}) + f(x_{dist.\ road\ it}) +$$

$$+ f(x_{east.\ it}: x_{north.\ it}) + \boldsymbol{\beta}_{year.month} + f(x_{east.\ it}: x_{north.\ it}): \boldsymbol{\beta}_{year.month},$$

where Y_{it} is the response variable for a given bird at time t, i.e., the presence or absence of a bird i at time t, and it can be written as $Y_{it} \sim Bernoulli(1, p_{it})$, where p_{it} is the probability of bird presence for bird i at time t. β_0 represents the intercept, $\boldsymbol{\beta}_{land\ cover}$ represents the vector of coefficients for land cover (one for each class of, up to 13), $\beta_{prot.\ area}$ represents the coefficient for (outside a) protected area, $\boldsymbol{\beta}_{pop.\ density}$ represents the vector of coefficients for population density (up to two). $\boldsymbol{\beta} f(x)$ represents the vector of coefficients for the quadratic B-spline associated with variable x. $f(x_{east.\ i}: x_{north.\ it})$ is a bivariate smooth of the spatial term constructed using a Gaussian radial basis function for a given bird i at time t; $f(x_{east.\ it}: x_{north.\ it}): \boldsymbol{\beta}_{year.month}$ is the interaction of this term with the temporal term, which allows a different set of coefficients for the bivariate smooth for each year-month combination, for a given bird i at time t.

Furthermore, the mean variance relationship for Bernoulli variable is known and

$Var\ (Y_{it}) = p_{it}(1 - p_{it})$; and the linear expression is achieved by a link function $g(\cdot)$, here the logit function, expressed as $logit\ (p_{it}) = \log({}^{p_{it}}/_{1 - p_{it}})$.

Model Setup

The flexibility of the univariate smooth terms (i.e., the number and location of knots) was automated using the SALSA method (Spatially Adaptive Local Smoothing Algorithm, [59]). The parameters set for SALSA1D were:

- minimum knots = 1,
- maximum knots = 3,

- selection criteria used: BIC,
- gap parameter = 0, except for distance to nearest road or rivers = 50 km and for temperature = 1 °C.

The bivariate smooth of the spatial term was based on the CReSS method (Complex REgion Spatial Smoother, [60]) with SALSA2D to determine the number and location of knots (the flexibility of the smooth, [22]). All models were fitted using the MRSea package v. 1.0.1 [61] in R version 3.6.0 [62], with RStudio v. 1.1.456 [85].

The standard implementation in the MRSea package for the interaction term uses the same candidate knot locations across each level of the interaction but the parameter estimates may vary. However, for this analysis, there were some year-month combinations whose spatial range (i.e., the monthly MBR) was completely separate to others and this created an estimation issue. The developers of MRSea therefore proposed a new framework for allocating the flexibility in the effect of the spatial-temporal term which proved extremely advantageous (Scott-Hayward *pers. comm.*). Rather than setting out 300 candidate knot locations, evenly spaced (via a space filling algorithm) through the full geographical range of each bird (as incorporated in the MRSea package [61]) candidate knots were placed throughout the geographical range of each year-month. Thus, each knot location was only relevant to a particular year-month and the parameters associated with these were only effective within that year-month. This new framework greatly reduced the number of parameters in the final model, as well as the computational time. Therefore, the parameters for SALSA2D were:

- number of candidate knot locations per year-month = 30 (locations specific to each monthly MBR),
- total number of candidates = number of year-months x 30,
- minimum knots = 2,
- maximum knots = 70,
- selection criteria: BIC,
- gap parameter = 0.

With the use of tagging data, it was highly probable that there would be a violation of the residual independence assumption and so to allow for the residual correlation, a sandwich estimator was used to return robust standard errors [110]. This inflated the standard errors appropriately so that the estimates of uncertainty were realistic. The panel structure used were bird-days which meant that

locations within a day were correlated but between days were assumed to be independent – assumptions which were checked in each case.

Model selection and assessment

The flexibility of the smooth terms (1 and 2D) was determined using the Bayesian Information Criterion (BIC, [84]). Covariate selection (smooth, linear, removed) was achieved using hypothesis testing (via a marginal ANOVA based on the Wald statistic), ensuring the appropriate robust standard errors were used. If a covariate was deemed to be non-significant in the model, the model was refitted excluding that covariate, i.e., the covariate with largest p-value if it exceeded 0.05 would be removed. This process was repeated until all covariates in the final model were statistically significant. Covariates were also tested for collinearity each time a model was (re)fit; no colinearity was ever detected though. Modelling and covariate selection was done with the MRSea package [61] and collinearity was tested using car package [144] in R [62].

For each bird, the resulting final model was assessed for goodness-of-fit using both visual and numerical diagnostics. The suitability of the correlation block was visually inspected using autocorrelation function (ACF) plots. In the case of binary data, plotting the observed against fitted values was not informative. As such, the overall model suitability was visually assessed by plotting the spatial distribution of the fitted values and respective residuals, with suitability characterised by no discernible patterns through space. Binary data is hard to assess namely in the case of the mean-variance relationship of the model residuals, so this aspect was not inspected [145].

Additionally, the accuracy of each final model was inspected based on the outcomes from a binary classification. In such classification, the binary input data (i.e., the presence and pseudo-absences) are contrasted with the output data (continuous predicted probabilities converted back to binary according to a set threshold) and four classification outcomes are produced in a confusion matrix (**Table 5-4**). Here, a presence was considered as a condition positive (CP) and an absence, a condition negative (CN). A true positive (TP) occurs when a presence is predicted and a presence was observed. A true negative occurs when an absence is predicted and an absence was observed. Also, a false positive (FP) occurs when a presence is predicted but an absence was observed; these are also known as Type I error. And a false negative (FN) occurs when an absence is predicted but a presence was observed, also known as Type II error.

Receiver Operating Characteristic (ROC) curves are based on statistical decision theory; they contrast the true positive rate (defined as the proportion of positive conditions classified correctly, out of all

the positive conditions recorded; TPR) as a function of the false positive rate (defined as the complement of the true negative rate (TNR), i.e., the proportion of negative conditions classified correctly, out of all the negative conditions recorded; FPR = 1-TNR) for different cut-off points (thresholds; [146]). TPR is also denoted as sensitivity, FPR also denoted as 100-specificity. The ROC curve returns the "best" threshold for converting the predicted probabilities into the binary classification, and corresponds to the best sum of sensitivity and specificity; these were extracted using the pROC package [147]. The confusion matrix was constructed using the caret package [148].

Table 5-4 Outcomes from a binary classification, where the input is the observed data (columns) and the output are model predictions (rows).

		data	
		Condition positive (CP) (*a bird presence in this thesis*)	Condition negative(CN) (*a bird absence in this thesis*)
prediction	Test outcome positive (OP)	True positive (TP)	False positive (FP); Type I error
	Test outcome negative (ON)	False negative (FN); Type II error	True negative (TN)

Graphical Outputs

Plots are provided showing the functional response of bird presence to each covariate. For a given covariate, predictions were made by selecting a range for that covariate and holding all other variables constant (at their median or commonest factor level for the presence only locations). The spatial term was not included as there is no biological meaningfulness in considering one central point of the range of distribution of a vulture. A parametric bootstrap (500 iterations), using the robust variance-covariance matrix, was used to determine the 95 percentile confidence interval for each relationship. This resulted in one functional response plot for each covariate included in the final model for each bird, having one model per individual vulture.

Predictions based on each of the final models were made to illustrate the seasonal distribution for each bird. This was achieved by generating georeferenced predictions of the probability of presence for the distributional range of each bird (i.e., the respective minimum bounding rectangle, MBR) for the three seasons. Three dates were chosen to represent the three seasons: 01-03-2017 for the hot wet season, 01-07-2017 for cold dry, and 01-11-2017 for small rain. These dates were used to generate

the dynamic variables (vegetation index, temperature and precipitation). In the case when a bird was not observed in those months of 2017, the predictions were made to the values from 2017 but were assigned to represent months from 2018. For example, vulture tag ID 5785 had data from August 2017 to November 2018 **(Table 5-1**); as such, the characterisation of the seasons was assigned to the months of March 2018, July 2018, and November 2017, even though the dynamic variable information was all from 2017.

The uncertainty around the predictions was illustrated based on the robust standard errors, and 1,000 parametric bootstraps from the model coefficients. The median of those predictions was used to represent the expected seasonal distribution. For visualisation, uncertainty was represented by the Coefficient of Variation (CV), specifically, one that is appropriate for variables with bounded scales (e.g., probabilities that are bounded by 0 and 1; $\mathrm{CV}_{\mathrm{bound}}$). The standard formula for the CV is the standard deviation divided by the mean, but this can give odd results when estimates are close to zero. Rather than using this convention, the denominator was expressed as:

$$CV_{bound} = [(X_{mean} - X_{min.})(X_{max.} - X_{mean})]^{1/2},$$

where X_{mean} is the mean of the predicted probability of vulture presence (across all seasons and locations), and $X_{min.}$ and $X_{max.}$ are the lower and upper bounds of the scale, 0 and 1 respectively [149].

All statistical procedures were implemented using R version 3.6.0 [62], with RStudio v. 1.1.456 [85]. Plotting was done mostly with the ggplot2 package [87] and also fields [114].

5.3 Results

5.3.1 Environmental covariates

Table 5-5 and **Table 5-6** illustrate the range of environmental conditions each bird encountered, and these values refer to the vulture locations only (i.e., presences).

Table 5-5 First of two tables describing the range of environmental conditions each bird encountered. These are summarised as: the variation in easting and northing (mean and range of variation per month; km); the percentage of locations recorded inside a Protected area (monthly mean and range; %); the prevalent land cover and population density class across months. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	yearmonth	Easting (km)	Northing (km)	Inside PA (%)	Land cover (class)	Population density (class)
5403	11	252.43 (144.19 - 461.57)	201.67 (126.08 - 522.25)	57.8 (39.8 - 81.78)	140	POP.2
5404	20	167.84 (47.99 - 370.07)	219.01 (53.32 - 645.65)	4.68 (0 - 23.25)	140	POP.2
5784	8	142.16 (105.39 - 172.95)	113.05 (96.25 - 145.92)	94.9 (87.14 - 100)	140	POP.2
5785	16	135.66 (79.25 - 189.61)	123.23 (69.12 - 165.24)	78.59 (68.96 - 87.79)	140	POP.2
5786	14	265.04 (44.06 - 432.42)	466.15 (75.68 - 813.34)	7.02 (0.23 - 40.32)	140	POP.1
5787	13	302.76 (72.1 - 916.97)	224.15 (55.27 - 546.29)	81.18 (12.19 - 100)	140	POP.2
5788	11	182.08 (148.51 - 323.85)	175.34 (87.11 - 239.24)	58.46 (41.01 - 77.99)	140	POP.2
5789	5	304.98 (180.7 - 514.98)	556.83 (168.37 - 1167.48)	1.81 (0.06 - 8.09)	140	POP.1
CAT1	13	53.01 (21.04 - 87.31)	84.93 (59.16 - 145.82)	98.73 (93.44 - 99.8)	130	POP.2
st2010-1330	14	40.16 (11.38 - 87.72)	69.59 (23 - 114.74)	99.56 (97.3 - 100)	60	POP.2
st2010-1332	35	178.76 (67.4 - 600.43)	125.23 (35.47 - 307.05)	95.59 (66.67 - 100)	140	POP.3
st2010-2607	21	253.19 (115.03 - 389.95)	178.21 (76.79 - 262.81)	40.95 (6.83 - 78.23)	140	POP.2
st2010-2608	17	136.42 (68.9 - 289.01)	113.88 (82.73 - 200.15)	95.16 (87.25 - 99.2)	140	POP.2
st2010-2609	11	226.84 (115.49 - 417.52)	187.29 (127.17 - 353.42)	87.68 (70.11 - 98.46)	140	POP.2
st2010-2697	15	193.99 (62.81 - 273.21)	201.74 (59.23 - 297.71)	20.95 (0 - 66.43)	140	POP.1
st2010-2700	18	404.17 (143.02 - 900.88)	365.82 (99.38 - 766.23)	13.39 (0 - 60.62)	140	POP.1

Table 5-6 Second of two tables describing the range of environmental conditions each bird encountered. These are further summarised as: the range of NDVI (monthly mean and range); the range of distances to the nearest river and to the nearest road (monthly mean and range; km); the range of elevation (monthly mean and range; km); the range of temperature (monthly mean and range; °C); and the range of precipitation (monthly mean and range; mm). Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	NDVI	Min. dist. river (km)	Min. dist. road (km)	Elevation (km)	Temperature (°C)	Precipitation (mm)
5403	0.28 (0.2 - 0.36)	248.59 (175.39 - 289.7)	82.09 (52.05 - 104.74)	1.18 (1.12 - 1.24)	43.53 (34.77 - 50.15)	0.27 (0 - 1.02)
5404	0.29 (0.2 - 0.41)	356.31 (195.25 - 418.93)	38.29 (12.97 - 90.98)	1.4 (1.24 - 1.51)	40.96 (31.58 - 52.88)	0.14 (0 - 0.71)
5784	0.23 (0.19 - 0.34)	206.83 (201.94 - 210.7)	123.91 (116.09 - 129.56)	1.13 (1.12 - 1.13)	49.99 (43.44 - 53.98)	0.38 (0 - 1.15)
5785	0.26 (0.19 - 0.48)	211.89 (199.93 - 228.3)	122.42 (106.66 - 143.82)	1.15 (1.14 - 1.17)	46.3 (34.79 - 53.01)	0.21 (0 - 1.1)
5786	0.22 (0.16 - 0.4)	345.23 (265.87 - 428.61)	52.08 (11.74 - 81.54)	1.3 (1.17 - 1.49)	44.57 (34.56 - 56.76)	0.09 (0 - 0.31)
5787	0.4 (0.24 - 0.52)	53.42 (5.47 - 189.12)	86.28 (24.1 - 125.42)	1.02 (0.96 - 1.19)	40.39 (32.79 - 50.49)	0.57 (0 - 1.83)
5788	0.25 (0.19 - 0.45)	216.81 (178.39 - 234.18)	139.1 (109.07 - 162.04)	1.17 (1.15 - 1.21)	47.78 (35.92 - 53.34)	0.27 (0 - 1.08)
5789	0.26 (0.2 - 0.48)	76.06 (48.64 - 112.88)	27.18 (15.24 - 47.11)	1.14 (1.08 - 1.19)	48.31 (38.92 - 52.48)	0.14 (0.06 - 0.26)
CAT1	0.51 (0.35 - 0.67)	4.88 (1.04 - 15.51)	10.57 (5.74 - 18.3)	0.98 (0.97 - 0.99)	36.33 (29.81 - 47.71)	0.78 (0 - 2.87)
st2010-1330	0.46 (0.31 - 0.65)	4.72 (1.78 - 13.03)	7.58 (2.37 - 15.11)	0.98 (0.97 - 0.98)	38.15 (31.53 - 47.1)	0.65 (0 - 2.12)
st2010-1332	0.41 (0.25 - 0.63)	18.63 (12.26 - 50.29)	28.92 (19.2 - 53.51)	0.97 (0.95 - 1.06)	39.94 (29.32 - 52.17)	0.7 (0 - 3.25)
st2010-2607	0.29 (0.2 - 0.55)	239.5 (172.93 - 312.38)	123.12 (69.19 - 149.52)	1.19 (1.15 - 1.27)	42.52 (32.06 - 53.05)	0.22 (0 - 1.18)
st2010-2608	0.26 (0.19 - 0.45)	200.14 (188.25 - 210.02)	108.44 (92.96 - 121.4)	1.12 (1.11 - 1.13)	45.13 (35.65 - 53.35)	0.28 (0 - 1.51)
st2010-2609	0.26 (0.21 - 0.42)	143.59 (131.1 - 163.34)	109.04 (79.65 - 123.09)	1.13 (1.12 - 1.14)	45.17 (35.91 - 52.81)	0.32 (0 - 1.38)
st2010-2697	0.28 (0.21 - 0.46)	289.07 (227.44 - 389.98)	105.63 (18.01 - 171.16)	1.27 (1.2 - 1.42)	41.5 (33.21 - 51.16)	0.22 (0 - 1)
st2010-2700	0.3 (0.19 - 0.48)	268.5 (40.47 - 475.45)	75.48 (23.1 - 164.49)	1.32 (1.13 - 1.6)	41.39 (32.7 - 51.4)	0.26 (0 - 1.8)

The variation in easting and northing was quite variable between birds, with differences also noticeable within birds; the variation was calculated as the difference between the extreme values

(maximum-minimum, **Table 5-5**). The highest mean variation in easting in a month was 404.17 km (by the sub-adult white-backed vulture, tag ID st2010-2700). The absolute mean maxima of 916.97 km (by the adult white-backed that travels between Etosha and Bwabwata National Parks, tag ID 5787; see distribution map **Figure II. 7** in the Appendix). Both the highest mean monthly variation in northing and the absolute maxima were recorded by the adult white-backed vulture tag ID 5789 (556.83 and 1,167.48 km, respectively). Furthermore, the widest mean monthly variation in both easting and northing was recorded by the white-backed *travellers* (defined as those birds that were seen more than 1,000 km away from their initial location, earlier in **Section 3.3.5**; tag IDs 5786, 5789, and st2010-2700), whereas the narrowest variation was recorded by the hooded vultures (tag ID st2010-1330 followed by CAT1).

The percentage of locations recorded inside a protected area in a month also varied considerably between bird (**Table 5-5**). Noticeably, three birds (17.65%) spent on average less than 8% inside a protected area (all adult white-backed), whereas five other birds (29.41%) spent more than 94% on average inside a protected area (three adult white-backed, and the hooded vultures). The variation within birds was also noticeable. Three birds in particular, showed a distinctly large range of percentage of monthly locations recorded inside a protected area (tag IDs 5787, st2010-2697 and st2010-2700). The most prevalent land cover class for all the white-backed vultures was “closed to open (>15%) grassland” (shown as class “140” in **Table 5-5**). The immature hooded vulture (tag ID CAT1) was seen mostly over “closed to open (>15%) shrubland (<5m)” (class “130”), whereas the locations from the adult hooded (tag ID st2010-1330) were mainly recorded on “open (15-40%) broadleaved deciduous forest (>5m)” (class “60). Most bird locations were recorded in areas of medium population density. The class “POP.2” was the most prevalent class for 11 birds (64.71%); among those birds were the two immature white-backed, and both hooded vultures. Only one adult white-backed vulture preferred areas of high population density (“POP.3”).

The monthly mean NDVI (vegetation index) was mostly between 0.20 and 0.30 across all birds (**Table 5-6**; low NDVI indicates few vegetation and higher values (close to 1) indicate a high density of green leaves). Nonetheless, only two birds recorded an absolute maximum below 0.40 (both adult white-backed, tag IDs 5403 and 5784), whereas five other birds recorded an absolute maximum above 0.50 (two adults and one immature white-backed, and the two hooded vultures). One of the immature white-backed (tag ID st2010-2607) showed the widest variation in monthly NDVI (0.20 - 0.55). Three of the birds were always recorded within 50 km of a river (one adult white-backed, and both hooded vultures). Additionally, six birds were always within 100 km from a road (four adult white-backed, and the hooded vultures). There was little variation in the topography of the locations recorded within bird. Comparing between birds, all but two vultures transmitted locations above 1,000 m in elevation

(both hooded vultures). Also, two white-backed vultures transmitted locations above 1,500 m (the adult tag ID 5404 and the sub-adult tag ID st2010-2700).

The land temperature of the vulture locations recorded, on the other hand, varied greatly (**Table 5-6**). Including all vulture locations, temperature ranged from 8.73 to 64.42 °C. Only three birds had a mean per month lower than 40 °C. The adult white-backed tag ID 5784 recorded the smaller variation (10.54 °C) and the adult tag ID 5786, the largest variation (22.20 °C). The study area was incredibly dry throughout most of the year (**Table 5-6**). The rain was limited to the Northern section of the study area during the hot wet season. From all vulture locations, precipitation ranged from nil to 37.30 mm. Two adult white-backed vultures never visited locations with more than a mean of 0.32 mm of rain in a month (tag IDs 5786 and 5789) while four out of the five birds that spent time around the Bwabwata NP had a monthly mean of at least 0.57 mm of rain (two adult white-backed, and the two hooded vultures).

Additional biological questions

Did individual vultures employ different strategies in exploring the surrounding environment? Did some vultures restrict their movements to also restrict their exposure to a large variability in the environmental conditions? Three white-backed vultures with contrasting movements were selected to start addressing these questions (**Table 5-7**).

As shown in **Chapter 4**: the adult tag ID 5785 stayed local to Etosha NP while the sub-adult tag ID st2010-2700 showed the largest variation in monthly home range, and the adult tag ID 5787 recorded the largest East to West movement (916.97 km, **Table 5-5**), having travelled repeatedly between Etosha and Bwabwata National Parks.

The overall range of variation per month in each of the variables monitored (calculated as $\Delta\, range = min_{range} - max_{range}$, taken from **Table 5-5** and **Table 5-6**) showed that the vulture that explored the smallest area was also exposed to the smallest variation in environmental conditions. The vulture that stayed local to Etosha NP had the smallest variation in all but two of the continuous variables- the vegetation index and temperature, which variations were quite similar for all birds. Conversely, the vulture that showed the largest variation in monthly home range also showed the largest variation in environmental conditions for 62.5% (five) of the continuous variables.

Table 5-7 Characterisation of the range of environmental conditions met by three exemplifying white-backed vultures. A brief description of the vultures is presented as well as transmitter identification (tag ID), age class, location of the tag deployment, start date of the vulture locations included in this analysis, and number of months each bird was monitored for. Also, the prevalent class per month is shown for each categorical variable; the range of variation per month ($\Delta\ \boldsymbol{range}$) and the overall monthly mean (in brackets) are shown for the continuous variables.

	Tag ID	5785	st2010-2700	5787
	Age	immature	sub-adult	adult
	Traveller/ local	local	traveller	NA
	Description	smallest variation in monthly home range	largest variation in monthly home range	movement between Etosha and Bwabwata
	Depl. Region	Etosha NP	Etosha NP	Bwabwata NP
	Start analysis	2017-08-01	2017-06-01	2017-11-01
	no. months	16	18	13
Habitat characteristics				
	Land cover (class)	140	140	140
	NDVI	0.29 (0.26)	0.29 (0.30)	0.28 (0.40)
	Min. dist. river (km)	28.37 (211.89)	434.98 (268.5)	183.65 (53.42)
	Elevation (km)	0.03 (1.15)	0.47 (1.32)	0.23 (1.02)
	Eastings (km)	110.36 (135.66)	757.86 (404.17)	844.87 (302.76)
	Northings (km)	96.12 (123.23)	666.85 (365.82)	491.02 (224.15)
Climate variables				
	Temperature (°C)	18.22 (46.3)	18.70 (41.39)	17.70 (40.39)
	Precipitation (mm)	1.10 (0.21)	1.80 (0.26)	1.83 (0.57)
Human presence				
	Inside PA (%)	18.83 (78.59)	60.62 (13.39)	87.81 (81.18)
	Population density (class)	POP.2	POP.1	POP.2
	Min. dist. road (km)	37.16 (122.42)	141.39 (75.48)	101.32 (86.28)

It may also be that some environmental features play a larger role than others for specific events. For example, do vultures use those features for navigation? To address this question, I focused on the four birds that performed longer trips.

Mapping the distances from the vulture locations to the main roads inside the study area revealed some individuals that performed long trips kept close to roads (**Figure 5-2**). Both vultures that travelled along the central meridian in Namibia (tag IDs 5786 and st2010-2700) kept at close distance from the roads (locations closer than 50 km, in darker cells in blue in **Figure 5-2**). Also, both individuals that travelled through Botswana seemed to show preference for road lines (**Figure 5-2,** two bottom plots; tag IDs 5789 and st2010-2700). The vulture that travelled between Etosha NP and Bwabwata NP might show some interest in roads but seemed to follow a straight latitudinal line when crossing the central section between the two National Parks (tag ID 5787). It was also visible on the bottom left map that the trip South via the West did not go as far as the main road, so perhaps animals also follow other habitat features (**Figure 5-2**). It could also be that vultures follow the roads to prey upon roadkill. This

was only a brief inspection to address the topic in question; more detailed examination would be necessary to be sure about the importance of roads to the navigation of vultures.

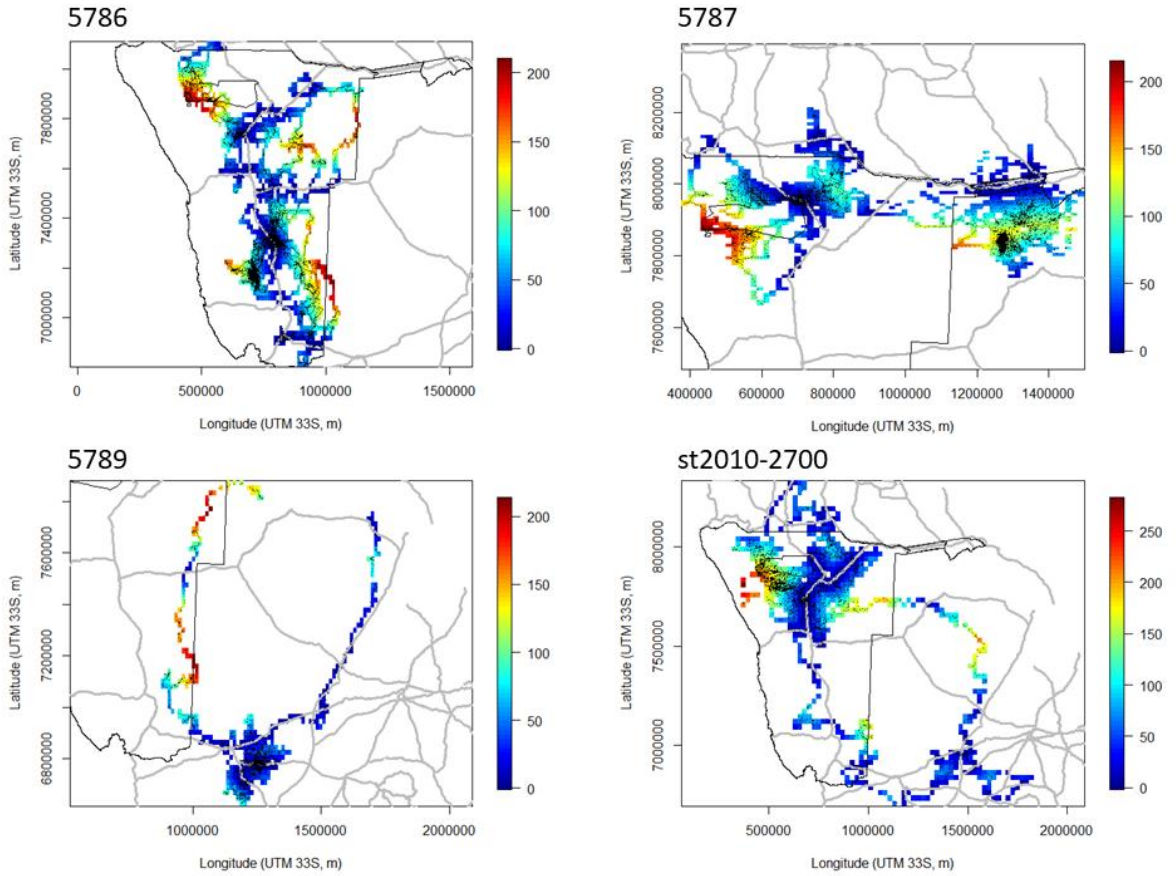


Figure 5-2 Maps showing the distances from vulture locations to the main roads inside the study area. Four vultures are shown for illustration, all having performed long trips (tag IDs 5786 and 5787 – top; tag IDs 5789 and st2010-2700 – bottom). Roads are shown in grey, bird locations in black and distances are shown in km and coloured from blue (close) to red. The border of Namibia, as well as Etosha and Bwabwata National Parks are shown in black, for reference.

Visits to protected areas

There were locations recorded by all 16 birds inside a protected area even though the number of those records differed greatly between birds (**Table 5-5**, **Figure 5-3**). Overall, 55.08% of all bird locations were recorded within a protected area. 28.57 % of locations were recorded inside Etosha NP (transmitted by 12 individuals), and 9.02 % of locations were recorded inside Bwabwata NP (transmitted by 4 individuals).

Vultures visited protected areas all throughout the year, with no apparent seasonal pattern (**Figure 5-3**). Temporal fluctuations were evident for most birds, as the percentage of locations recorded inside a protected area varied between months. Nonetheless, that oscillation was minimal for both hooded vultures (tag IDs CAT1 and st2010-1330) which generally spent more than 93.40 % of time within Bwabwata NP and its surrounding protected areas.

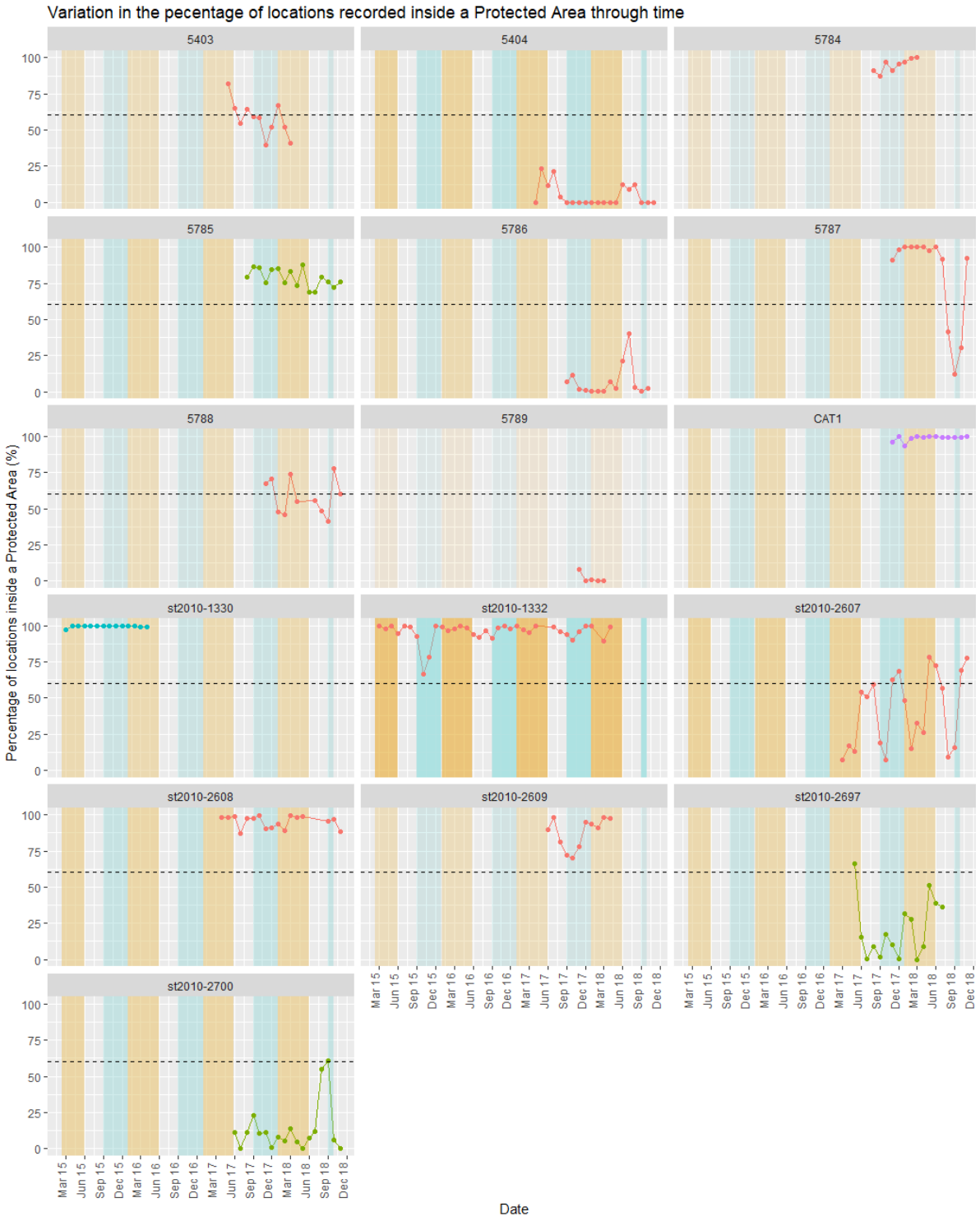


Figure 5-3 Variation in the percentage of locations per month recorded inside a protected area, for each bird through time (%). Individuals coloured by age class and species: adult white-backed vultures in red, immature and sub-adult in green; immature hooded in purple; adult hooded in blue. Seasons along the year coloured differently: hot wet in golden, cold dry in grey, small rain in blue. Dashed horizontal line represents the overall DDT mean.

Figure 5-3 shows clearly the point when vulture tag ID 5787 travelled West leaving Bwabwata NP and the surrounding protected areas behind (see movement in its monthly home range in **Figure VI. 6**). There was a dip in the percentage of locations recorded inside a protected area between July and October 2018, when this vulture travelled towards Etosha NP and explored its surroundings, mostly farmland. Vulture tag ID 5786 and 5789 spent minimal time within a protected area, travelling through areas with no conservation protection (**Figure VI. 5** and **Figure VI. 9**). Vulture tag ID st2010-2700 showed more interest in the areas surrounding Etosha NP with only a peak in August and September 2018, when its core areas overlapped with Etosha NP (**Figure VI. 32** in the Appendix). Interestingly, vultures tag ID st2010-2607 and st2010-2697 showed an evident fluctuation through time, especially the former. Both vultures alternated between areas in- and outside Etosha NP, exploring both a National Park and farmland.

5.3.2 Habitat modelling

Model results

Eleven covariates were initially included in the habitat models for each vulture, with only a small number of covariates not exhibiting evidence for a genuine relationship with the probability of presence of a vultures (**Table 5-8**). Only one final model retained all covariates (that for tag ID st2010-1332), eight models (50%) excluded one covariate, and seven (43.75%) of models deemed two or three covariates not statistically significant, in light of the other covariates included in the model.

Overall, the covariates included in the habitat models were considered useful in predicting the probability of presence of vultures throughout the study area. That is, each covariate was deemed statistically significant according to the ANOVA-based tests, at least at a marginal level of 5% (p-value < 0.05). All birds retained vegetation index (NDVI), distance to nearest river and road, as well as the spatial and temporal terms (**Table 5-8**). Two of the covariates were excluded from eight final models (50%), inside or out of a protected area and precipitation (cells highlighted in blue in **Table 5-8**). Population density was excluded from five final models (31.25%), and three other covariates were excluded from one final model – land cover, elevation and temperature. The vast majority of the covariates were deemed highly statistically significant (p-value < 0.001) in the final models (82.95%, highlighted in green in **Table 5-8**).

The number of classes in the categorical variables varied slightly between birds; this resulted from the data preparation when at times classes needed to be merged (see **Section 5.2.2** for more detail). The

categorical variables were highlighted with "*" in **Table 5-8**: the temporal term, inside or out of a protected area, land type, and population density. The variation in the number of classes was noticeable on the number of monitoring months (bird-months). However, the interpretation of this variable was not to be done independently of the geographical coordinates, as the final models included an interaction between those temporal and spatial terms. All continuous variables retained in the final models were fitted as smooth terms suggesting the relationship between each and the response variable was non-linear. These were applied to NDVI, distance to nearest river and road, elevation, temperature and precipitation. These six covariates were present in the 16 models (one for each bird); in 10 occasions the covariate was excluded from the model (10.42% of those 96 occurrences). Given the covariate remained in the final model, 67.44% had three or four degrees of freedom, while the remainder 32.56% took the maximum flexibility allowed (five degrees of freedom).

The covariates included in the habitat models for both hooded vulture (tag IDs CAT1 and st2010-1330, highlighted in blue in **Tab. 5-8**) were indistinguishable from those selected for the white-backed vultures.

Table 5-8 Summary of the variables included in the models to analyse habitat preferences, for each vulture individually. Variables included in the models as categorical are highlighted with a "*"; all other were included as continuous. Cells are colour coded by the level of statistical significance of each variable in the final model: blue- excluded, salmon: marginally significant (p-value < 0.05), green- highly significant (p-value < 0.001). Number inside the cells indicate the degrees of freedom: number of classes minus one, for the categorical variables; number of knots chosen in the final model, for the continuous variables. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	Date * (year-month)	insidePA *	LandCover *	Population *	NDVI	MinDistRiver (km)	MinDistRoad (km)	Elevation (km)	Temperature (°C)	Precipitation (mm)	Geographic coordinates
5403	10	1	8		4	5	5	5	5	3	35
5404	19		8	2	3	5	5		3		43
5784	7		7	1	3	4	3	3		3	41
5785	15	1	8	1	5	5	4	5	4		43
5786	13		8	2	5	5	5	4	5	4	41
5787	12	1	9	2	3	5	4	4	3		51
5788	10	1	7		5	5	5	5	3	3	49
5789	4		6		3	5	3	3	4		43
CAT1	12		7	1	3	3	3	5	3		37
st2010-1330	13	1	7	1	3	3	3	5	5		37
st2010-1332	34	1	7	1	3	4	3	3	3	3	34
st2010-2607	20		6	2	3	5	3	4	3		40
st2010-2608	16		6	1	3	5	5	3	3		26
st2010-2609	10	1	6		3	3	3	5	3	3	41
st2010-2697	14			2	3	5	4	3	5	3	43
st2010-2700	17	1	7		3	4	4	4	4	3	38

Model assessment

The final model for each bird was assessed, both visually and numerically. **Figure 5-4** to **Figure 5-6** illustrate the visual diagnostics performed, using bird tag ID st2010-1332 (the only model that retained all covariates, as mentioned above) as an example. The autocorrelation function plot (ACF, **Figure 5-4**) showed a good decay on average, within each autocorrelation block comprising "bird-day". The candidate knots showed good spatial coverage, located generally where the monthly geographic ranges mostly overlapped (**Figure 5-1**). The number and location of knots chosen each month varied, with no knots chosen on 19 (54.29%) of the 35 months (from the 30 candidate knots each month). The model performed well, as seen in the maps with the fitted values (the estimated probabilities of vulture presence, **Figure 5-5**) and respective raw residuals (**Figure 5-6**). The former shows a good agreement with the observed vulture locations (shown in black) and the latter shows only a few traces of those locations.

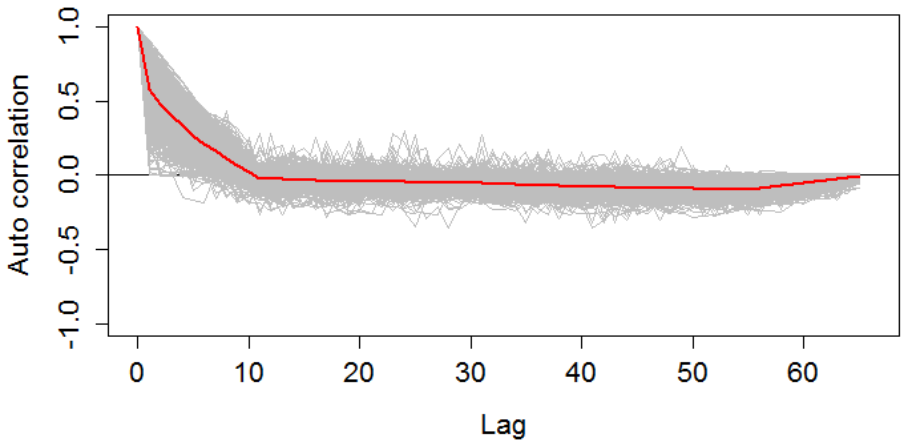


Figure 5-4 Visual diagnostics performed on the final model for bird tag ID st2010-1332 – autocorrelation function (ACF) plot, where each lag represents a vulture location in a given day.

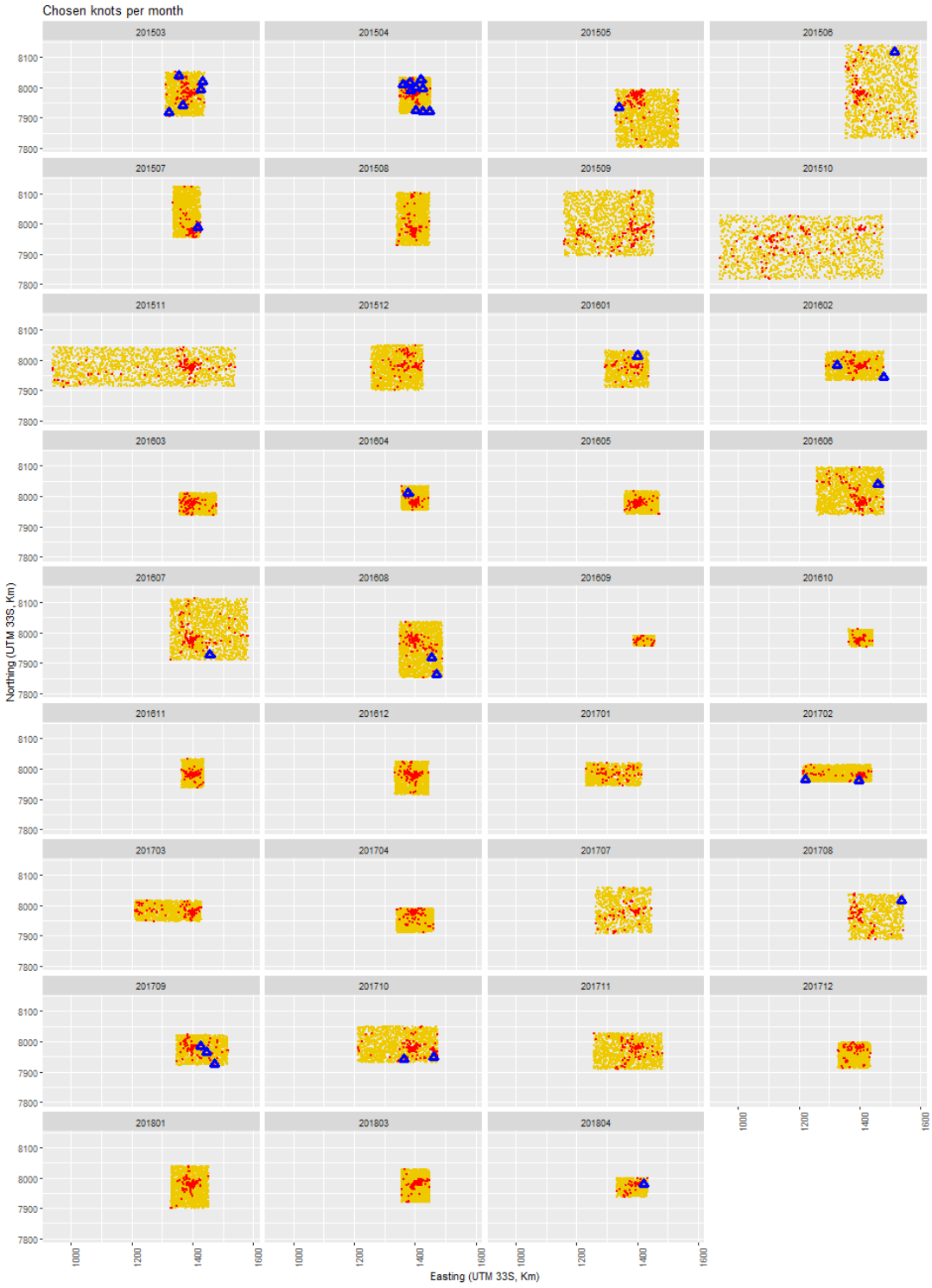


Figure 5-1 Visual diagnostics performed on the final model for bird tag ID st2010-1332 – chosen knots for each year-month (blue triangles), shown with the vulture presences (in red) and pseudo-absences (golden).

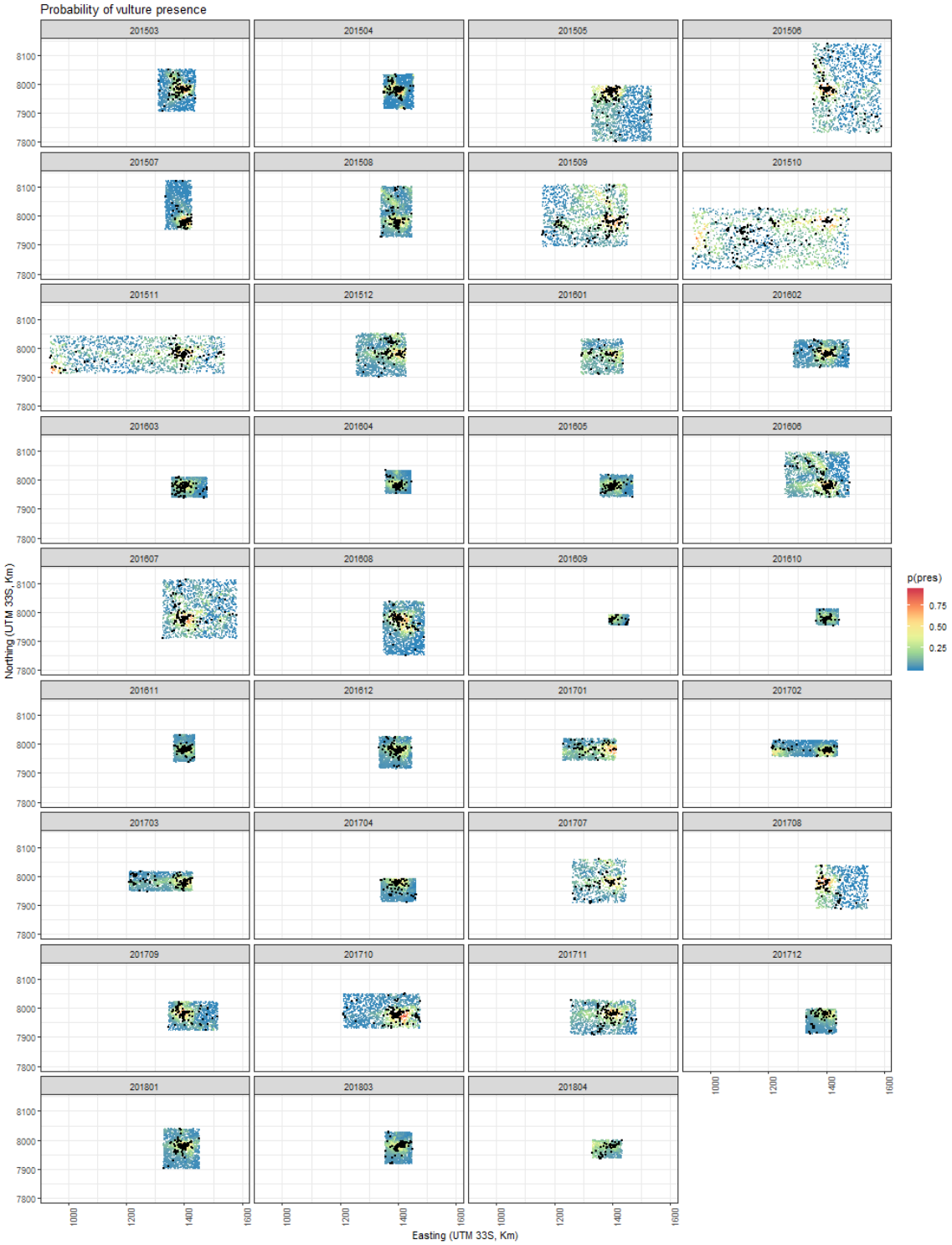


Figure 5-5 Visual diagnostics performed on the final model for bird tag ID st2010-1332 – estimated probabilities of vulture presence (in the range of blue to red), with locations (in black points), shown for each year-month.

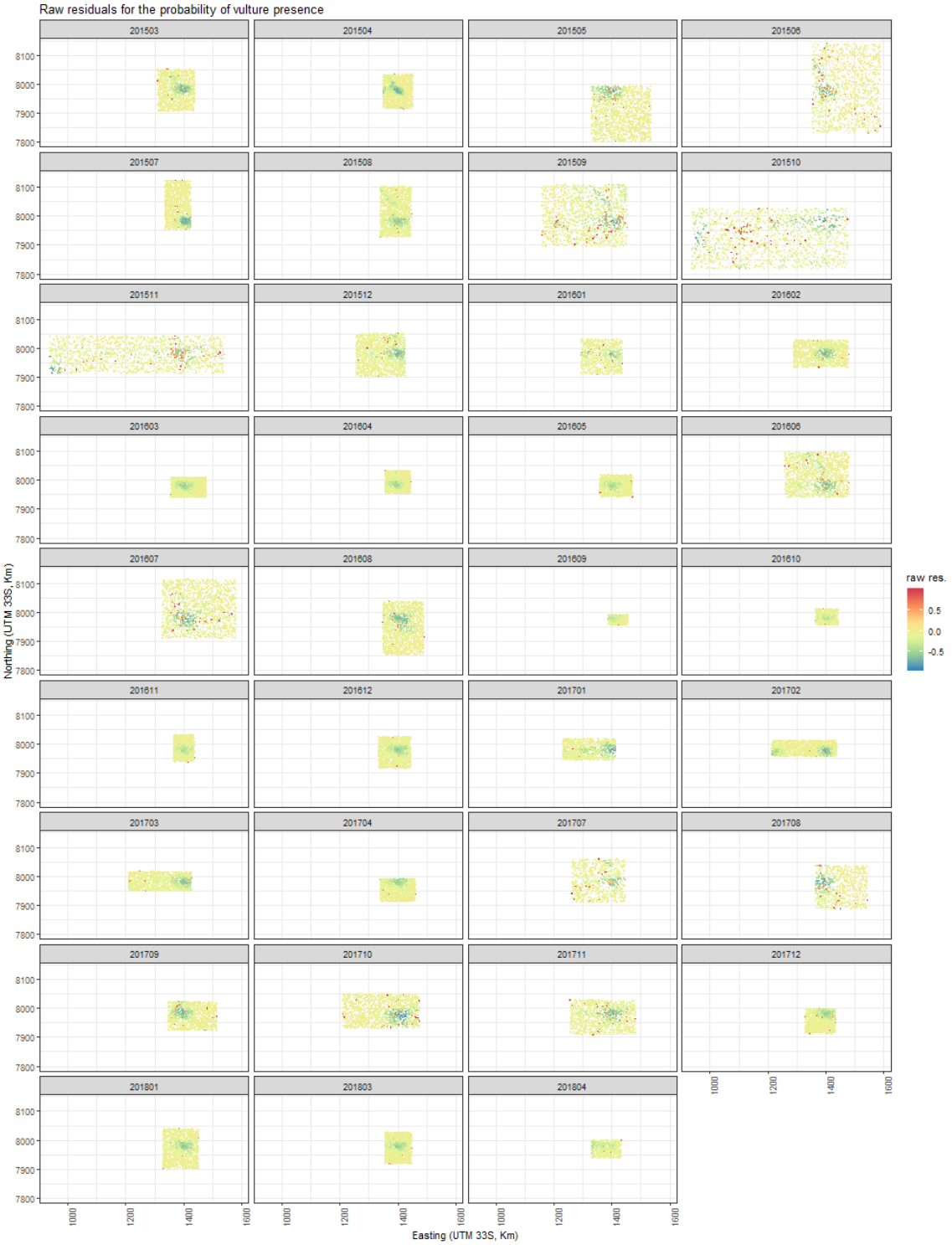


Figure 5-6 Visual diagnostics performed on the final model for bird tag ID st2010-1332 – estimated residuals associated to the probabilities of vulture presence (in the range of blue to red), shown for each year-month.

Furthermore, the observed values were contrasted with the predicted outcomes (converted to binary values using the method described in **Section 5.2.4**). The accuracy and relevant associated statistics

for each of the final models are shown in **Table 5-9** (refer to **Table 5-4** for further definitions). Accuracy is defined as the proportion of conditions classified correctly (provided with a 95 % confidence interval, CI); sensitivity is defined as the proportion of positive conditions (i.e., the presences) classified correctly; specificity is the proportion of negative conditions (i.e., the pseudo-absences) classified correctly; positive predictive value represents the probability that the positive test outcomes truly refer to positive conditions; negative predictive value represents the probability that the negative test outcomes truly refer to negative conditions; the detection rate is the proportion of true positives in the data; and the detection prevalence is defined as the proportion of test outcome positive.

Overall, the accuracy of the models was high (**Table 5-9**). All models showed an accuracy greater than 0.70 with four models exceeding 0.80. The sensitivity and specificity of the models showed a similar range of values; the former varied between 0.70 and 0.90 and the latter varied between 0.67 and 0.87. The negative predictive values outnumbered the positive predictive values, but the data was also built with five times more pseudo-absences (negative condition) than presences. The detection rate ranged between 0.12 and 0.15 which was reasonable given the probability of presence was 0.17. Lastly, the detection prevalence ranged from 0.25 to 0.42 which again, was reasonable; if we attributed up to 0.17 to true positives we would still get a small proportion of false positives.

The accuracy of the models for both hooded vultures (tag IDs CAT1 and st2010-1330, highlighted in blue in **Table 5-9**) were indistinguishable from the results obtained for the white-backed vultures.

Table 5-9 Summary of the assessment of the performance of the final model for each bird, expressed as the accuracy (with 95 % CI) and relevant associated statistics – sensitivity, specificity, positive predictive value, negative predictive value, detection rate, and detection prevalence. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	Accuracy (95% CI)	Sensitivity	Specificity	Pos. pred. value	Neg. pred. value	Detection rate	Detection prevalence
5403	0.702 (0.699, 0.706)	0.848	0.673	0.342	0.957	0.141	0.414
5404	0.753 (0.751, 0.755)	0.729	0.757	0.375	0.933	0.122	0.324
5784	0.799 (0.797, 0.801)	0.794	0.800	0.443	0.951	0.132	0.299
5785	0.802 (0.780, 0.803)	0.773	0.808	0.445	0.947	0.129	0.289
5786	0.778 (0.776, 0.780)	0.742	0.785	0.409	0.938	0.124	0.303
5787	0.764 (0.762, 0.767)	0.778	0.761	0.395	0.945	0.130	0.328
5788	0.737 (0.735, 0.740)	0.837	0.718	0.372	0.956	0.140	0.375
5789	0.823 (0.820, 0.827)	0.897	0.809	0.484	0.975	0.150	0.309
CAT1	0.787 (0.785, 0.789)	0.863	0.772	0.431	0.966	0.144	0.334
st2010-1330	0.858 (0.853, 0.862)	0.819	0.865	0.549	0.960	0.137	0.249
st2010-1332	0.803 (0.799, 0.806)	0.695	0.824	0.443	0.931	0.116	0.263
st2010-2607	0.707 (0.702, 0.712)	0.830	0.682	0.343	0.953	0.138	0.403
st2010-2608	0.779 (0.773, 0.784)	0.769	0.781	0.412	0.944	0.128	0.311
st2010-2609	0.781 (0.776, 0.787)	0.817	0.774	0.420	0.955	0.136	0.324
st2010-2697	0.768 (0.764, 0.772)	0.832	0.755	0.405	0.958	0.139	0.343
st2010-2700	0.717 (0.714, 0.721)	0.746	0.712	0.341	0.933	0.125	0.365

Functional responses

The effect each covariate had in explaining the probability of presence of vulture (given all other covariates) was assessed visually. Even though each bird had its own set of prediction values, some remarks can be made.

The median values for all covariates were generally very similar for every bird with only a few notable exceptions (**Table 5-10**). From all the final models that included inside or out of a protected area, only one contained the median outside one such areas (model for vulture tag ID st2010-2700). Also, the median nearest distance to rivers or roads, were far smaller for the two hooded than for all the white-backed vultures.

Table 5-10 Summary of values attributed to each covariate when determining the functional response curves for each bird. The median was used for the continuous variables and the most prevalent class was used for the categorical variables. (*) indicates the variables were excluded from the final model. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	Date	insidePA	LandCover	Population	NDVI	MinDistRiver (km)	MinDistRoad (km)	Elevation (km)	Temperature (°C)	Precipitation (mm)
5403	2017-12	1	140	(*)	0.258	250.285	85.659	1.138	45.180	0.047
5404	2018-08	(*)	140	POP.3	0.2631	393.5313	32.31556	(*)	40.30539	(*)
5784	2018-01	(*)	140	POP.2	0.214	213.518	121.294	1.122	(*)	0.000
5785	2018-03	1	140	POP.2	0.229	204.322	111.191	1.129	47.537	(*)
5786	2018-05	(*)	140	POP.1	0.186	384.580	37.539	1.236	43.971	0.000
5787	2018-08	1	140	POP.2	0.383	23.001	88.792	0.974	39.909	(*)
5788	2018-10	1	140	(*)	0.214	224.557	138.257	1.156	50.313	0.000
5789	2017-12	(*)	140	(*)	0.208	58.602	17.669	1.138	50.734	(*)
CAT1	2018-03	(*)	130	POP.2	0.521	1.409	5.250	0.977	34.077	(*)
st2010-1330	2015-08	1	60	POP.2	0.451	1.778	2.913	0.979	38.457	(*)
st2010-1332	2016-03	1	140	POP.3	0.396	14.525	23.791	0.957	38.554	1.569
st2010-2607	2017-08	(*)	140	POP.2	0.238	245.191	128.780	1.167	41.386	(*)
st2010-2608	2017-07	(*)	140	POP.2	0.230	202.028	104.536	1.117	46.201	(*)
st2010-2609	2017-07	1	140	(*)	0.249	139.341	117.220	1.115	42.455	0.000
st2010-2697	2017-05	(*)	(*)	POP.2	0.245	276.032	142.739	1.264	38.793	0.000
st2010-2700	2017-06	0	140	(*)	0.261	287.845	59.652	1.298	39.947	0.000

The shape of each functional response may change for a given covariate for different birds. It can also be distinct for each covariates of a given bird. In broad terms, if a functional response remains a flat line it suggests the probability of bird presence is effectively unchanged regardless of the value of that covariate. Furthermore, if the shape of the plot varies remarkably (and accounting for the confidence

interval bands), it may also suggest preference or avoidance of a bird to a range of values of the respective covariate.

All functional responses for each of the covariates included in the final model for each vulture are presented in **Appendix VIII**. Here those plots for vulture tag ID st2010-1332 that retained all the environmental variables considered are shown (**Figure 5-7**). Note, the tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (i.e., a presence, the 1's) and pseudo-absence (0's).

The plot for the temporal term (bird-month) had little meaning as this term was included in the final models as an interaction with the spatial term (i.e., the geographic coordinates; **Figure 5-7** top left). Keeping all variables constant except the type of land cover suggested this adult white-backed vulture had less preference for areas dominated by "closed (>40%) broadleaved deciduous forest (>5m) (class "50"). Also, this vulture had less preference for areas outside protected areas (class "0"), and for areas with moderate human density (class "POP.2"). There was a general decline in the relative probability of presence (relative p(pres)) as NDVI increases whilst the opposite was true for temperature (as temperature increased, so did the relative p(pres)). There was an increase in relative p(pres) close to rivers (0-20 km), roads (10-25 km) and at low elevations (500 and 700 m high). The relative p(pres) increases again as minimum distance to road and elevation increased and there was a second peak for minimum distance to road at approx. 100 km, although the uncertainty was much higher. The relationship with precipitation was a slow increase in relative p(pres) to about 15 mm rain and then a decline in relative p(pres) as precipitation increased.

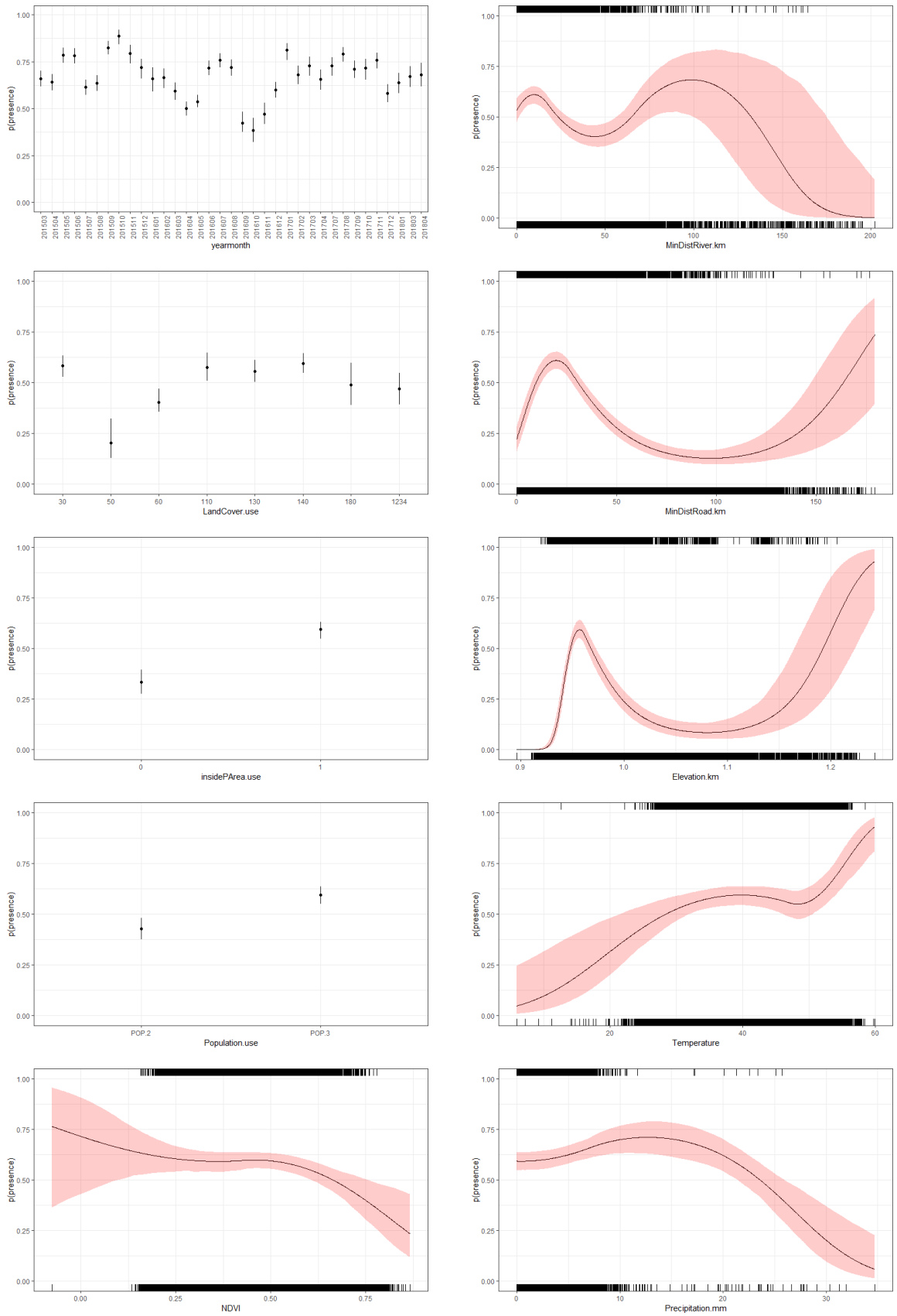


Figure 5-7 Functional response for covariate included in the final model for bird tag ID st2010-1332. From the top: nearest distance to river (km), and to road (km), elevation (km), temperature (°C), precipitation (mm); vegetation index (NDVI), population use, in/ out a protected area, land cover, year-month.

Moreover, the shape of the functional responses could also highlight patterns between individuals. Contrasting four examples for the same covariate (here, distance to nearest river), showed that birds that occupy a similar geographical range might also show similar patterns in the functional responses (**Figure 5-8**). The two plots on the left hand side refer to vultures that spent their time locally, in and around Etosha NP (tag IDs 5785 and st2010-2608). Both vultures showed a preference for distances of approx. 200 km from rivers. The high uncertainty for the larger distances to a river reflected the lack of support from the observed data (note the fewer tick marks on the top of the plots). Contrastingly, the two plots on the right hand side on **Figure 5-8** refer to vultures that travelled a long way, through contrasting environmental conditions (tag IDs 5787 and st2010-2700). These two vultures were observed at a noticeably larger range of distances from a river (from 0 to more than 450 km), the shapes of the functional responses were smoother with larger associated uncertainty, especially in the case of tag ID 5787.

Even though the plots on the right hand side are quite distinct from those on the left, it is interesting to note that the vulture with tag ID 5787 might have also shown a peak at distances of approx. 200 km from rivers (top right on **Figure 5-8**). Lastly, the vulture with tag ID st2010-2700 which showed the largest variation in monthly home range and travelled widely through the study area, had the least variable preference for proximity to rivers of the examples shown in **Figure 5-8**.

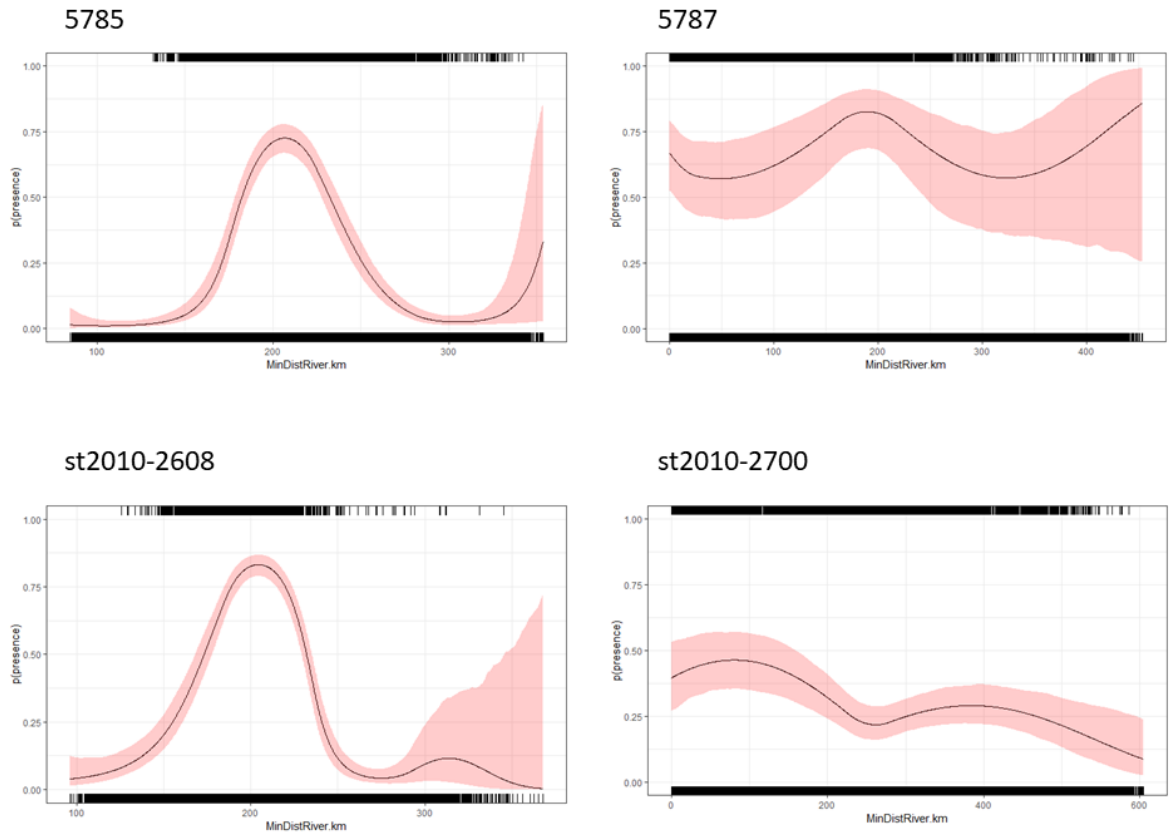


Figure 5-8 Illustration of contrasting shapes obtained in the functional response, here exemplified for the distance to the nearest river for birds with tag IDs 5785, 5787, st2010-2608 and st2010-2700. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

Further statistical considerations

The vast majority of the functional responses seem to perform well. There were nonetheless, some patterns that may indicate to pitfalls on the approach taken. Four examples were highlighted on **Figure 5-9**. The plot on the top left shows a sharp increase in elevation with unrealistic biological meaning, followed by a high statistical uncertainty. This might have been fixed by constraining the proximity of the allocation of knots in the model (via the gap parameter). The plot on the top right illustrates an unreasonable large uncertainty, perhaps originated in part by the lack of presence data along the range of precipitation values in the model (note the narrow cluster of tick marks on the top of the figure). The plot on the bottom left shows perhaps an unnecessary oscillation at higher elevations, possibly resolved by restricting the degrees of freedom allowed to this covariate. Lastly, the bottom right plot might show a relative probability of bird presence for close proximity to roads higher than anticipated; there seem to be support from both presence and pseudo-absence data, suggesting a

more average relative p(pres) would be anticipated. However, none of these patterns were of great concern.

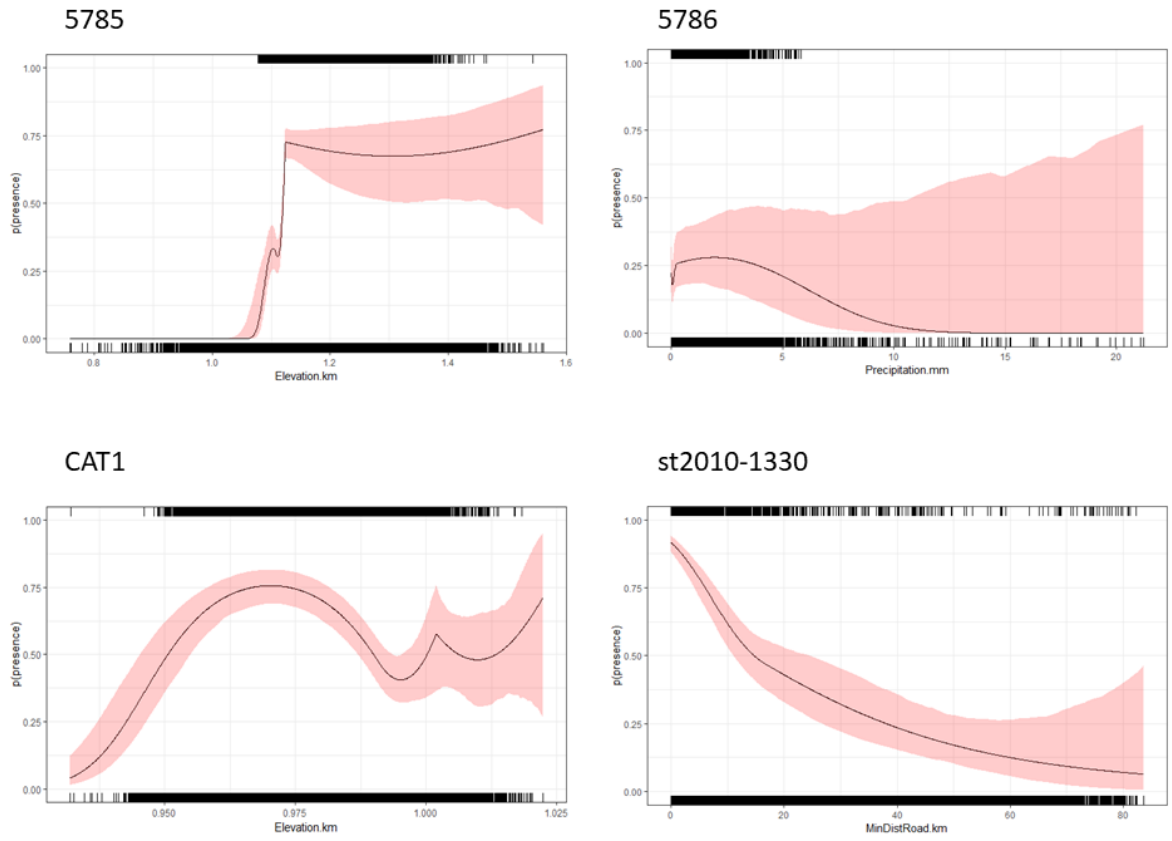


Figure 5-9 Illustration of contrasting pitfalls obtained in the functional response, here exemplified for three covariates in the final model of four birds. The functional responses shown are: elevation for bird with tag ID 5785 (top left) and tag ID CAT1 (bottom left), precipitation for tag ID 5786 (top right), and distance to nearest road for tag ID st2010-1330 (bottom right). The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

Predictions

The predictions made to illustrate the seasonal distribution for each bird seem agreeable. The uncertainty around those predictions was only high on a few patches which did not overlap with the areas of higher predicted vulture presence. All predictive maps, shown with the expected median relative probabilities of vulture presence (resulting from the parametric bootstrap), as well as the respective maps with the associated uncertainty, measured as the Coefficients of Variation

appropriate for bounded variables (CV_{bound}), are shown in **Appendix IX**. Once again, the example chosen is that of bird with tag ID st2019-1332 (**Figure 5-10**).

The expected relative probabilities of this vulture presence, informed by the characterisation of its habitat in each of the seasons showed a good scattering over the range areas. These prediction maps also highlight an area of potential higher importance for this white-backed vulture, located at the SE corner of Bwabwata NP. The uncertainty associated to the predictions was quite low, the lowest recorded for any given prediction set (CV_{bound} ranged between 0.01 and 0.11).

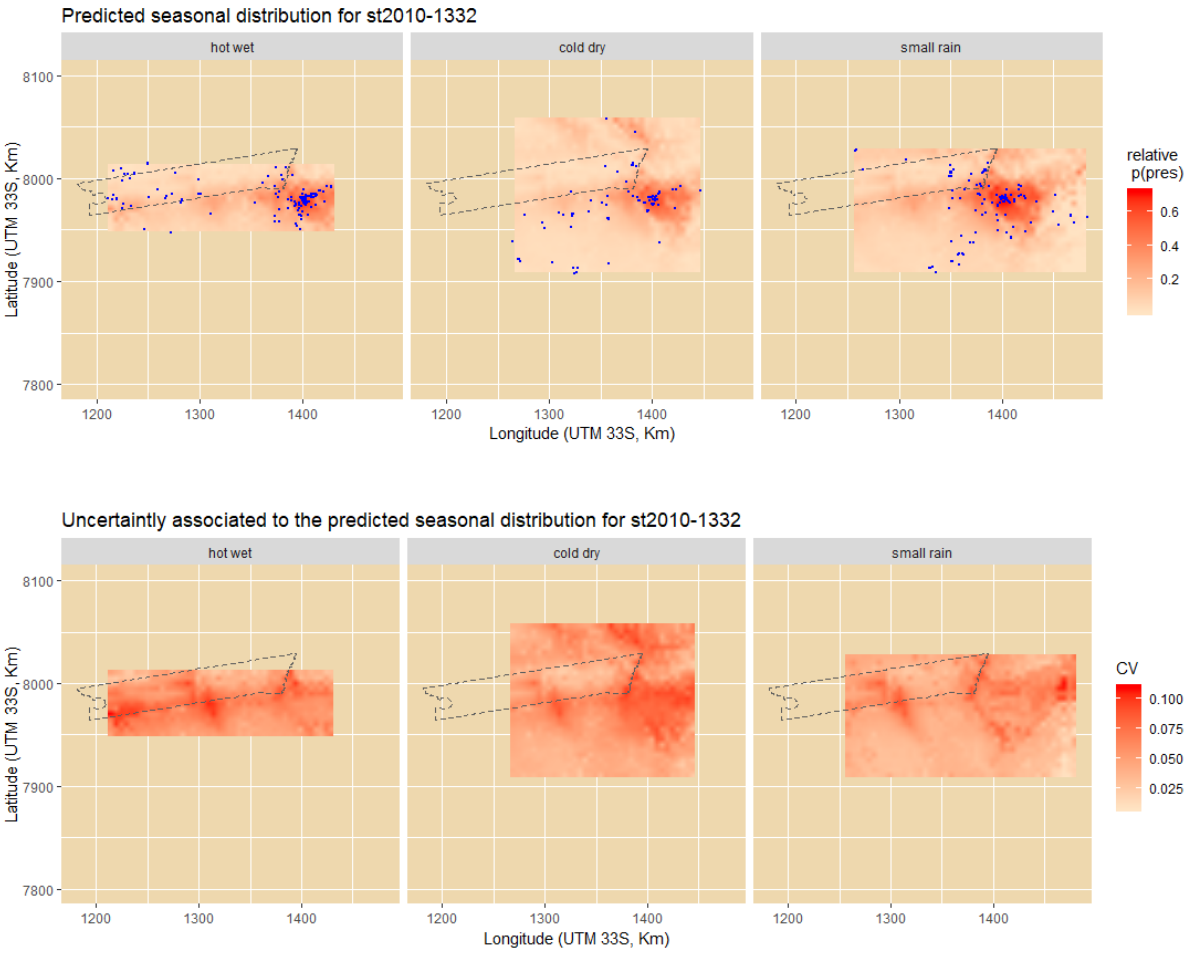


Figure 5-10 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture tag ID st2010-1332. Borders of Bwabwata National Park shown for reference.

Further statistical considerations

Most of the prediction maps seemed sensible with some exceptions being discussed here. There were nonetheless, some patterns on the CV maps that could deserve further investigation. **Figure 5-11** showcases two examples. The top maps show the uncertainly for the predictions made to the cold dry season (middle maps; tag ID 5404) had three patches of high values ($\mathrm{CV}_{\mathrm{bound}}$ ranges between 0.005 and 0.998). On one hand these were not of great concern because they fell on areas of low predicted (relative) presence of vulture; this may have resulted from the calculation of the $\mathrm{CV}_{\mathrm{bound}}$ in which dividing very small amounts will generate a large CV. As such, this would have no biological significance. On the other hand, those patterns may signal some underlying instability on the final model that originated the predictions. It was visible that the size of the range areas in each season varies greatly, with that for the cold dry season being exceptionally large; perhaps further adjustments to the model parameters could be made to accommodate such variation in the range areas.

Contrasting, the predictions made for another white-backed vulture do not extend through such varying geographical areas, nor do they have such large uncertainty ($\mathrm{CV}_{\mathrm{bound}}$ ranges between 0.007 and 0.666). But there seems to be large uncertainty in areas of predicted vulture presence, again for the cold dry season (bottom middle maps; tag ID st2010-2608). This vulture spent most its time in the central – western sections of Etosha NP with only a few locations recorded in the surrounding areas. There may perhaps be some small scale environmental conditions that were not well captured by the final model contributing to uncertainty in the resulting predictions.

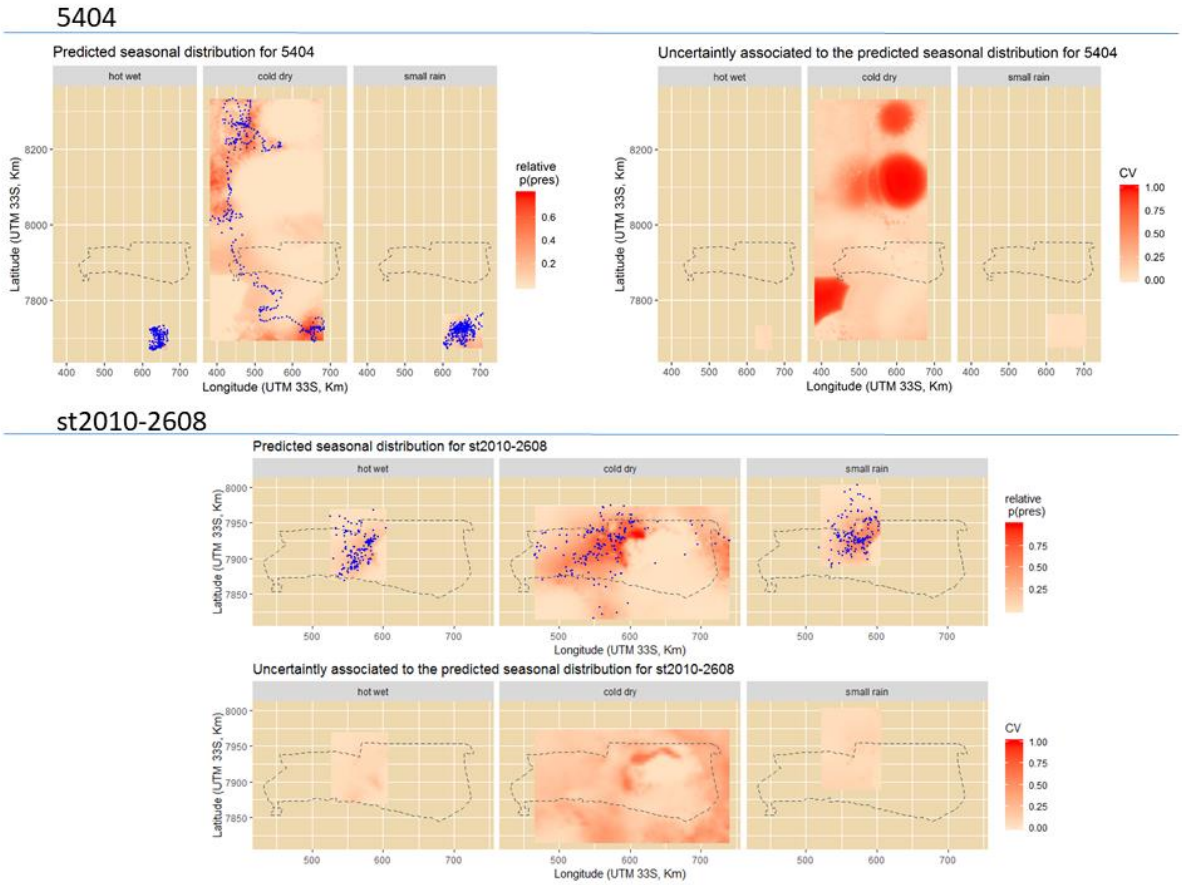


Figure 5-11 Illustration of pitfalls obtained in the prediction maps and associated uncertainty (Coefficient of Variation, $\mathrm{CV}_{\mathrm{bound}}$). Examples shown from the final models for vultures with tag ID 5404 (top maps) and tag ID st2010-2608 (bottom maps). The same scale of $\mathrm{CV}_{\mathrm{bound}}$ is shown to allow comparison between maps.

5.4 Discussion

The analysis of habitat preferences provides an indication of how species relate to their environment. This is important not only to understand the ecology of species but also to guide conservation and management measures. Information about the environment can be gathered *in situ* (e.g., weather stations on the ground) but remote sensing is key in the case of studies of highly mobile species, over large or remote areas. There is a vast amount of data derived by remote sensing and its accessibility has been greatly facilitated by automated annotation systems. The Environmental-Data Automated Track Annotation (Env-DATA) is one example and delivers the characterisation of the geo-referenced animal locations under study [122].

Environmental covariates

In this study nine environmental covariates were investigated to model the habitat preferences of African vultures. All those covariates relied on satellite imagery as not only was the study area quite extensive (2.3 million sq.km), it was also remote. Covariates were chosen based on known relevance in previous studies and described habitat characteristics, climate variables and indices of human presence.

A key concept of macroecology is that more abundant and widespread species (such as vultures) tend to be more broadly tolerant of environmental conditions [150]. Environmental variables that made flight more energetically cost-effective have been related to larger home ranges in vultures, while proxies for increased food availability prompted smaller home range [12, 150]. It has also been suggested that most attention has been given to migratory populations, with the need to address resident populations [150]. A characterisation of the environmental conditions each vulture encountered in the present study showed different levels of environmental variation. This is not surprising given the differences found in both the size and the geographical extent of their range areas (**Chapter 4**). From the contrast made between three vultures, the one that showed narrower ranges of variation per month was also the vulture that stayed local to Etosha NP. This was only a brief inspection but could nonetheless, begin to uncover whether individual vultures employed different strategies in exploring the surrounding environment. It may also represent an initial baseline for future, more detailed studies on environmental plasticity with important considerations in light of scenarios such as Climate Change.

The individual characterisation of the environment also highlighted how some features can play larger roles at times. The main roads inside the study area were of special importance for the individuals that performed long trips, often navigating at close distance from the nearest road. A study along the roads of SW South Africa found raptors (namely, white-backed vultures) and corvids were recorded more often foraging in road verges or flying along roads, than foraging or flying over rangelands [151]. The authors pointed out that roads and their verges through arid and semi-arid areas often generate high production systems. These have also been highlighted as breeding and foraging habitats, as well as movement corridors for vertebrates. Furthermore, animals involved in road collisions could also provide food for carrion-feeding animals [151]. In turn, scavengers are vulnerable to becoming roadkill themselves. Vultures have been recorded among the species of roadkill [151]. Many avian scavengers learn to be aware of traffic and fly off on vehicle approach, however, increasing avian traffic casualties raises conservation concerns about rare and threatened species [152].

The contrast made between three selected vultures, also showed varying ranges for elevation. The birds that travelled farther visited locations with larger variation in elevation than the vulture that stayed local to Etosha. Elevation may also play a role in movement and navigation. Not only do topographical features shape the landscape, but the importance of elevation has been shown for flight strategies of soaring birds [153, 154]. Weather and topography go hand in hand and the importance of weather conditions on the flight behaviour and efficiency has been shown for several bird species around the world. Such relationship between weather features and flight characteristics has been address for migratory journeys, such as for turkey vultures in America [150], Golden eagle migrating through North America [155], and several migratory birds in Israel [153]. It has also been addressed more locally within the Serengeti National Park (Tanzania) for species such as white-headed and hooded vultures [156]. This may therefore be an important consideration to shape future work and assess the variations in habitat usage with flight conditions.

Habitat modelling

All environmental covariates considered in this study were important to explain the probability of presence of vultures within the study area. The methods implemented were statistically robust and the resulting predictions showed good agreement with the observed data. The inclusion of the bivariate smooth term also showed that the environmental covariates inspected were not generally sufficient alone to explain the presence/ absence of a vulture along their monthly geographical range. However, there were no knots allocated to the bivariate smooth on 54.29% of the months analysed, indicating the probability of presence was being well captured by the environmental covariates included in the models. Each bird related to their environment in its particular way, with some similarities at times and overall the patterns recorded for the two hooded vulture were indistinguishable from those of the white-backed. There was also no perceptible differentiation between the vultures carrying transmitters deployed in Bwabwata National Park (NP) from those deployed in Etosha NP. This is not surprising given the small sample sizes in terms of species and age class and the large variability in movement between individuals (as shown in the previous **Chapters 3** and **4**).

As a whole, the three most important covariates in explaining the probability of presence of vultures were vegetation index (NDVI), distance to nearest river and distance to nearest road. These three were retained in all final models. The NDVI variable provides a good approximation of vegetation density. It is frequently used as an index of primary productivity and has been proven useful in sparsely vegetated areas. Turkey vultures in America reduced their home ranges at times of high productivity,

when the need to forage for food was lower [122]. Prey abundance is often indicated as the main drive of the habitat use of predator species, although in the case of scavengers the abundance of prey mortality may also have an important contribution.

In fact, NDVI has been highlighted as an important predictor to map the occurrence of anthrax [157] in Kruger NP (South Africa). The mechanisms of propagation of the spore-forming bacterium *Bacillus anthracis* are complex and still being explained [158] but environmental indices link the pathogen to grazers and to the presence of scavengers [157]. Anthrax has been monitored in Etosha NP for over four decades showing most cases occur in the wet season, especially between February and May [116]. The movement of herbivores has been linked with anthrax areas, namely elephants and zebra herds which largely migrate away from such areas of Etosha during the anthrax season. Furthermore, scavengers such as the white-backed vulture play an important role in anthrax dynamics, by tearing open carcasses and promoting blood flow into the soil [158]. A study in Kenya showed vultures favoured the proximity to migratory herds when those herds experience their highest mortality, during the dry season [96]. White-backed vultures in the Masai Mara National Reserve preferred greener areas (evidenced by NDVI) all through the year. The authors suggested the species may have a closer dependence on prey abundance than the lappet-faced and Ruppell's vultures, shaping the differences between these overlapping species. Differences in habitat use are important for coexisting vultures, more so during periods of reduced food availability such as the wet season [96].

The analysis in this chapter showed each vulture had a slightly different relationship with NDVI (keeping all else constant) even though most showed a preference for higher NDVI. It was noted each vulture used habitat with ranging NVDI and the recorded values agree with the land type the birds most likely used. Individual mean NDVI values were between 0.20 and 0.30 which agrees with the main type of land use present in the study area (Closed to open (>15%) grassland). It also agreed with the geographic location as birds with higher NDVI were recorded around Bwabwata NP, an area known to be greener. No links can be made at present with regards to the motivations driving those relationships between the probability of presence of a vulture with NDVI. Nonetheless, given the predictive power of this vegetation index in explaining the occurrence of both prey distribution and prey mortality (through the monitoring of anthrax for example [157]), it would be worth pursing such links in future work.

Also important in explaining the probability of presence of vultures was the distance to nearest river and distance to nearest road. Dean and Milton (2003) showed that the high biodiversity that gathers by the roads and their verges represents a source of food for scavengers [151]. The distance to nearest

river has also been shown to be influential in studies such as mapping habitat preference for nesting of white-backed vultures [117]; white-backed vultures often nest along rivers.

Furthermore, the least important covariates assessed in this chapter, in light of all the covariates considered in the models, were inside or out of a protected area and precipitation; these were not deemed important for half the vultures. On one hand, all but one of the birds tagged in Bwabwata National Park are among the individuals for which precipitation was excluded. The park is located in the richer section of the study area in terms of access to water; several perennial rivers intersect its boundaries and the Okavango Delta is not far South. It is well known that the dynamic shifts in flooding patterns, from permanent streams and swamps to dry woodlands nurture a wealth of species diversity in the Delta [159]. This may suggest that precipitation was deemed non important for some birds that had access to water in other ways. On the other hand, precipitation might have been best considered in the models with a time lag. A study has found that the abundance of large raptors such as the white-backed vulture was more affected by rainfall from the previous year [160].

Even though all birds recorded locations inside protected areas, this covariate was not important for half the vultures in this study (considering all the other covariates assessed). This may be in part because the study area is vast and remote. Despite 25.90% of the study area cells intersecting with a protected area, only 0.76% of the study area had more than 100 persons/ sq.km and just 0.14% was covered in urban areas. This suggests the anthropogenic pressure was altogether low. Furthermore, the protected areas were included regardless of its characteristics. Areas differed in IUCN management categories, governance or ownership type; additionally, each country may impose their own regulations. It could be that the vultures flew over the environment not differentiating an area with protection from another without. These findings agree with those of a previous study that looked at the movement of immature white-backed vultures tracked from the North West Province of South Africa [39]. Those birds were also recorded within the Western section of the study area in this study, having flown all the way up North. The immature vultures rarely visited protected areas in South Africa even though they spent extended periods around the Kavango-Zambezi Transfrontier Conservation Area (TFCA). As a reminder, the Kavango-Zambezi TFCA encircles the Bwabwata NP (where five tag deployments took place) and extends through all neighbouring countries, i.e., Angola, Botswana, Namibia, Zambia and Zimbabwe [89]. Authors have suggested that preference might have been due to the higher densities of ungulate and the low anthropogenic disturbance in those areas outside South Africa [36, 39, 161, 162].

Only one vulture in this study showed preference for densely populated areas. This was an adult white-backed vulture (tag ID st2010-1332) that was mostly recorded in the far NE region of Namibia where several countries meet and there are a number of towns and small cities. It may have been then that this vulture took advantage of local landfill or abattoirs. There were in fact a number of other vultures that fed repeatedly on commercial farms or abattoirs in Namibia, perhaps also the case in its neighbouring countries but the knowledge of the area there was more limited. It has also been shown that the movement patterns of migratory species can alter in response to continuous availability of food resources on landfill. Some white stork (*Ciconia ciconia*) in Europe are now resident and rely on these anthropogenic sites for foraging year-round, especially when other food resources are scarcer [163]. The land cover classification incorporated in the models did not provide much detail about the land use and future work could try to address this point. Previous studies that have monitored the provision of food in supplementary feeding sites have shown vultures can visit those sites regularly [39, 164]. It has also been suggested that vultures could alter their foraging behaviour in response to such sites [39].

Further considerations for species conservation

Despite the fact that overall only 55% of all vulture locations were recorded inside a protected area, at the individual level the importance of such areas was unquestionable. Just over half the vultures (52.94%) transmitted at least 81.78% of their locations from within a protected area in a given month. This high usage of protected areas was recorded by individuals of both species, adult and immature, with tags deployed both in Etosha and Bwabwata NP. Overall, vultures seemed to show preference for the Northern section of the study area, but restraining their movements to Namibia. Interestingly, both here and in a study of immature white-backed tracked in South Africa [39], birds seemed to show little preference for Botswana. Despite the low population density in both countries, there may be higher densities of ungulates inside Namibian national parks where it is known that carcasses are left untouched and available for scavengers (G. Shatumbu, *pers. comm.*). **Chapter 4** showed vultures divided their time between Namibian protected areas and its surrounding agriculture and tourism farms where natural carcasses are also left available [90].

Both hooded vultures spent most their time in close proximity of the Chobe river (also called Cuando in Angola, and Kwando in Botswana). Locations were recorded not only inside Bwabwata NP but also on other protected areas across the border, through the Kavango–Zambezi TFCA. Even though their movements were more restricted than those of the white-backed vultures, the two birds selected for the results showcase how mobile species can utilise cross-boundary territory. Among the challenges

pointed for transboundary conservation and management actions are the varied laws and unequal human resources [165]. It has also been shown that consistency in listing status of species is beneficial for their effective conservation. The information about movement and habitat preferences such as that presented here are vital to fulfil that requirement.

Only three (adult white-backed) vultures showed little preference for protected areas. They each, unsurprisingly, showed distinct movement patterns. Nonetheless, they were all quite mobile and seemed to show preference for agriculture and tourism farms that do not always dispose of natural carcasses, as well as landfill and abattoirs around the cities. One such bird may have even built a nest on farmland as discussed in **Chapter 4**. Further illustrating how vultures are able to adapt their foraging behaviour in response to food provision and reduction of competition between conspecific [39, 96].

To conclude, this chapter has found that once more each bird showed individual patterns in the utilisation of its surroundings. Remote sensing data made readily available for analysis was crucial to characterise the extensive and remote study area in this work. Vultures exhibited tolerance to a suite of environmental conditions and the differences between birds extend with the findings from the previous **Chapter 4**. Birds showed such varied range areas and those that stayed more local were also exposed to less varying conditions. These observations will be relevant in future studies that address scenarios under Climate Change.

Interestingly this chapter described how some vultures showed attraction to roads, perhaps benefiting from the richness that gathers at road verges. Wind conditions have also been highlighted as a key aspect for flight strategies, and could be an important addition in future characterisation of range areas. Nonetheless, all nine environmental covariates included in the models proved to be important in explaining the probability of presence of vultures throughout their monthly range areas. Unsurprisingly, the level of importance varied between birds. The vegetation index (NDVI) and nearest distance to road and river were the most important covariates, agreeing with previous studies and linking vultures to the potential abundance of prey mortality. Special mention was made to the distribution of anthrax given its relevance for both wildlife and human welfare.

Even though inside or out of a protected area was deemed non important for half the vultures in this study, considering all the other covariates included in the models, the importance of such areas was reiterated. Diverse strategies for resource acquisition were discussed, once more evidencing how

birds may choose their path to minimize competition, perhaps, with other birds. The use of the Kavango-Zambezi region agreed with previous studies and supports the value of collaborative studies and the creation of transboundary initiatives. Despite the additional challenges in planning conservation for mobile species, it has been pointed that planning should explicitly account for the movement of individuals [166]. The data presented in this chapter discusses the habitat suitability of each individual vulture analysed. The relationships between each covariate considered and the probability of bird presence, as well as the seasonal predictive maps (with the respective uncertainty estimates) all help to increase the knowledge of these African vultures and can therefore provide the basis for tailoring future conservation plans.

6 General discussion

This thesis explored aspects of the ecology of movement of two free-ranging and critically endangered species. It described the movement patterns of the tagged African vultures at an unprecedented level of detail. It showed how variable vultures can be in the way they interact with their surroundings which significantly extends the current knowledge on white-backed and hooded vultures. The main findings are described in this concluding chapter, and their biological significance discussed. The findings and outputs generated from this thesis have sound statistical support and direct application in both conservation and management actions. Those applications are discussed, as well as prospects for future work.

6.1 Movement ecology

How, why, when and where do white-backed and hooded vultures move? These questions motivated the work developed in this thesis as it extended what was currently known about these critically endangered species. The thesis adopted the integrative framework termed "movement ecology" [1].

The thesis inspected movement at different time scales, for each bird separately. Daily distance indices based on consecutive locations recorded within a bird-day were examined (**Chapter 3**). Monthly area indices were described based on the range areas most utilised in each bird-month (**Chapter 4**). Environmental data were then incorporated to provide a characterisation of the monthly range areas and assess the importance of habitat features for the movement of the study species (**Chapter 5**).

Movement reflects a dynamic interplay between both internal and external factors to the individuals [1]. The metrics generated in this work were inspected in light of such factors. Internal factors relate to physiological and behavioural characteristics of each bird; these were not measured in this thesis but related examples were identified in the literature. Observational studies would be one way to ground truth some of the explanations proposed in the literature to date. Nonetheless, the large variation found within each bird as well as between birds was consistent across the metrics inspected. This consistency strongly supports the concept that personality influences the way individuals perceive their surroundings, as they gather spatial information to build their "cognitive maps" [79].

External factors include habitat structure and locations of key resources, predators and enemies [4]. These were initially alluded to using reports from preceding studies (**Chapters 3** and **4**) and later formally assessed using environmental covariates that related the vulture presence with habitat characteristics, climate variables and proxies for human presence (**Chapter 5**). External factors also include predators and enemies [4]. The study species are medium- (hooded vultures) to large sized (white-backed vultures) avian scavengers which are only occasionally predated on as immatures, by carnivores such as the black-backed jackals (*Canis mesomelas*) [44]. In terms of enemies, both these species are social, face competition from other larger species (such as the lappet-faced, *Torgos tracheliotos*) but tend to congregate in large numbers with no known causalities [40, 45]. The two study species though, as well as vultures in general, have been facing severe population declines greatly due to human presence [32] and sentinel poisoning in particular; with this in mind, proxies for human presence were included in the habitat modelling and special emphasis is given to the overlaps with protected areas present in the study area (more on **Section 6.2**).

It was challenging to put the results of this thesis in context with preceding studies that touched on aspects of the movement ecology of the study species. There were only a small number of relevant reports and the lack of movement information was especially scarce for the hooded vultures. This can be explained by two main factors. One is that each study will have its own aims and methods for data collection and analysis. The other is precisely the nature of the data. To the best of our knowledge, only in the past decade have satellite-based transmitters been attached to vultures in Southern African countries, the number of deployments are not large in number and the results have not yet been made public. This is showcased by the 30 transmitters that have been attached to hooded vultures in six African countries between 2013 and 2017. Even though there is a joint analysis made to the resulting 604 bird-months [92], only information for 4 deployments made in Botswana have recently been made available [98].

The challenge was also further complicated by the different methods used to estimate home range and core areas. The various methods available to estimate range areas produce differing results making comparison between previous studies harder [100, 105], even when extending their taxonomic and geographic ranges. Moreover, failing to address the autocorrelation inherent in geo-referenced location data which has dominated the already sparse literature to date, intensifies disparities in results and almost no results exist which are based on methods that necessarily address the autocorrelation issue.

The methods implemented throughout this thesis adequately captured the autocorrelation structure in the data, given the model. Thus, they generated results and associated uncertainty (95% confidence intervals), which are both accurate and realistic in their uncertainty. The volume of the data analysed with the thorough methodological approach taken here, also generated an unprecedented set of detailed results on the movement ecology of the study species.

The initial visual inspection of the overall locations showed vultures extended their movements differently. Some stayed more local to Etosha or Bwabwata National Parks (where all but one deployment took place) while others flew over neighbouring countries (Angola, Zambia, Zimbabwe, Botswana and South Africa). Most interestingly, the general pattern of movements around Etosha NP agreed with that detected 10 years ago during the only other preceding study in Namibia [73]. One other study based in the North West Province of South Africa showed each of the six immature white-backed vultures extended through areas of distinct area and shape [39]. This also agrees with the findings presented in this thesis that showed striking differences in the range areas between birds. What this thesis also found was that not only did the immatures performed long exploratory flights as widely suggested in the literature (e.g., [39, 44]); adults did too. Three adults travelled farther than five times the (two) immature birds did, reaching up to a maximum of an unprecedented 1,628 km away from its initial deployment location (recorded by the sub-adult in 188 days). This triggered further comparison between the movement strategies of white-backed vultures and the speculation about the differentiation between two groups: *travellers* and *locals*. Despite the mixture of daily metrics between birds, with temporal variation seen in all individuals and each showing its own pattern, the *travellers* performed occasional long-range trips. The *locals* on the other hand, were always contained within a far smaller area, even though they recorded large daily distances. Those long-range forays could reflect an adaptive exploratory foraging strategy to acquire remote food resources or potential mates for breeding. The characteristics of such movements could also explain the lack of synchronisation found between conspecifics [73]. This differentiation was illustrated with contrasting examples but not formally tested. Also, no such appreciation was possible for the hooded vultures as only two birds were present in this study.

However, despite the mixture of results at the individual level, the mean of most movement metrics for the (two) hooded vultures were smaller than the respective means for the (17) white-backed vultures. The lack of statistical significance separating these species in this case (which we speculate is due to the small number of individuals and high uncertainty which produced the relatively wide overlapping 95% confidence intervals) does not allow the observations in this study to extend what

has already been reported but still, it seems to support that smaller birds move within smaller areas [115].

The lack of clear similarities in the movement strategies between birds was carried over as analysis progressed. Clear variations were seen within birds through time in both daily and monthly metrics, with differing patterns between individuals. Also, clear discrepancies in both the size, shape and geographic location of their monthly range areas were apparent. Despite the lack of information about the breeding status of the adult white-backed vultures in this study, the monthly range maps were inspected in light of the timing when white-backed vultures lay their eggs (between April and June in central Namibia, [43]). While all results are provided in this thesis, two birds were contrasted to illustrate how the expansion and contraction of the range areas could be linked (at least for one bird) with the time vultures would need to spend more time in a nest. This led to the suggestion that there may be both breeding and non-breeding adults (*floaters*) among the study birds. Even though no references were found for the existence of floaters among white-backed vultures, those are present in many other bird populations, and evidenced by the separation during the breeding season between territorial (breeding birds) and non-territorial (the so called “floaters”, [11, 119]).

Another very interesting novel finding was that core areas vary far less than home ranges. The temporal variation of those metrics recorded by the two most contrasting birds showed that the mean core area (CA) varied far less than the respective home ranges (HR). Additionally, the mean CA/HR of those two birds focused on in particular was different but the 95% confidence intervals around such estimates overlapped. This could mean that:

- the lack of clear patterns between birds reflects the unpredictable availability of prey for African vultures [12], or expresses individual behavioural personalities [70];
- some birds can display large expansions in their home range areas, perhaps owed to difference in the resources available in the range areas, or motivated by the exploratory behaviour of those birds to exploit remote resource patches [73];
- other birds restrict their range areas due to their reproductive status, known to dictate the movements of African vultures [97]; and
- the little variation in the mean ratio CA/HR might be dictated by body size, animal fitness and/ or the efficiency in finding shelter and key resources [79].

Lastly, the remarks made thus far also extend to the way each vulture utilised their range areas. Each vulture showed its own relationship with the environmental covariates selected to assess habitat preferences during each bird-month. Overall, birds moved within a vast study area of more than 2.3 million sq.km (25 times larger than the area of Portugal) with a suite of environmental conditions that no doubt shaped some of the movement strategies found. Each vulture faced a different set of environmental conditions. The differences found in the environmental characterisation made per bird could be integrated with the predictive maps generated, and represent an initial baseline for future, and more detailed, studies on environmental plasticity. Such predictive maps showing the probability of presence of a given bird within the respective geographic range under a suite of conditions could allow important considerations in light of scenarios such as Climate Change. In keeping with the thoroughness kept all through this thesis, the predictive maps were associated with an appropriate measure of uncertainty, in this instance determined via a Coefficient of Variation appropriate for binary data, such as that analysed here [149].

All but one bird showed a preference for areas of low human density however, this could be a reflection of the small representation of areas with high human density in Namibia; only 0.76% of the study area contained more than an average of 100 persons/ sq.km. Even though inside or out of protected areas was not deemed to be important for half the individuals, the importance of such areas was unquestionable at the individual level. Vultures also utilised areas of neighbouring countries such as in the Kavango-Zambezi region supporting the importance of transboundary initiatives. Special emphasis was given to these results in light of the aims of the thesis, and these are discussed further in the next Section.

6.2 Species conservation

The ecological importance of vultures as a unique guild of obligate scavengers has been widely recognised among the researcher community [30, 31, 34]. Such importance has also been placed at the top of the international conservation policy agenda with a plea for urgent action [32, 35]. Moreover, a recent assessment of priority areas for conservation highlighted a concentration of highest priority areas for vulture conservation in southern Africa [35].

A Multi-Species Action Plan was created with the input of stakeholders, conservation and species experts, aiming to cease the population declines of 15 African-Eurasian vulture species [32]. Two of

the objectives and recommendations set from the Action Plan will guide some of the discussion of relevant findings of this thesis.

"To ensure availability of suitable habitat for vultures to nest, roost and forage"

The animal locations analysed in this thesis spanned over a wide area of Southern Africa. The field work was conducted in Namibia but this country only represented 35% of the overall 2.3 million sq.km of the study area. Georeferenced locations were reported mostly throughout Namibia but also over its five neighbouring countries - Angola, Zambia, Zimbabwe, Botswana and South Africa. The body of work presented in this thesis has therefore the potential to inform transnational management and conservation actions.

A characterisation was made of the study area using environmental covariates that were also used to assess the presence of each vulture throughout its range areas. Each vulture showed its own relationship with each of the covariates inspected but overall, the three most important covariates in explaining the probability of presence of vultures were vegetation index (NDVI), distance to nearest river and distance to nearest road. NDVI is a commonly used index of primary productivity and has been used to relate resource availability to the movements of turkey vultures *(Cathartes aura*); birds reduced their home ranges, in America, at times of high productivity, when the need to forage for food was lower [122]. NDVI has also been important to link the movement of migratory herds of wildebeest (*Connochaetes taurinus*) with the seasonal movement strategies from white-backed vultures, lappet-faced and Ruppell's (*Gyps rueppellii*) vultures in the Mara-Serengeti ecosystem of East Africa [96].

Also, vegetation type and distance to nearest river have been used to identify suitable habitat for foraging and breeding of white-backed vultures in different locations in Africa [117, 167]. *Bamford et al.* also included levels of protection to inspect both direct and indirect disturbance by humans on the suitability of nesting habitat [117]. To illustrate also the relevance of the other covariates deemed important for most vultures in the habitat modelling performed in this thesis, raptors (namely, white-backed vultures) and corvids were recorded more often foraging in road verges or flying along roads, than foraging or flying over rangelands in South Africa [151].

These other studies included the same key covariates incorporated in the habitat modelling in this thesis. This highlights that this work has incorporated predictors that have also been useful in other systems, perhaps facilitating the transferability of results. It may be that the main difference between this and the vast majority of the other studies is the large scale of the study area characterised in this

thesis. Even though raptors often occur over large areas and over diverse habitat types, studies have often focused on a relatively small geographic scale as is the case of all but one study cited in the previous paragraph (migration of turkey vultures in the America continent [122]).

"To support vulture conservation through crosscutting actions that contribute to addressing knowledge gaps"

The large volume of high resolution geo-referenced locations analysed in this thesis unquestionably bridged gaps in the knowledge about movement ecology of African vultures. The thorough statistical methods implemented adequately captured the structure of the data and produced estimates of movement metrics and probabilities of vulture presence with associated measures of uncertainty (95% confidence intervals and Coefficients of Variation). This means that the results presented in this thesis are unbiased and accurate but also realistic in their uncertainty and as such can be reliably used to underpin conservation action measures.

The approach taken in this thesis was to centre the analysis on each individual bird. Metrics were assessed at a range of time scales that could inform actions targeting more immediate or longer term processes. For example, the range of daily distances travelled found could be informative in assessing the likelihood of birds to visit supplementary feeding stations. Such feeding stations are widely used in some parts to sustain conservation programs or reduce high risk of intoxication by poisoning [12]. On the other end of the temporal spectrum included here are maps which detail all individual locations. These could be used to assess overlaps with human structures such as energy generation and transmission infrastructure and therefore help evidence the risk of collision. Extensive work has been done to assess the impacts of such structures both in land and at sea, namely using similar analytical approaches as the one implemented in this thesis [64].

Focusing on the geographic scales of the outputs of the present work, the monthly range areas provide valuable information both for management and conservation actions. Assessing overlaps between the higher areas of habitat usage for a species with those of a process or structure of interest, not only measure the likelihood of potential impacts on the species, but can also guide mitigation measures to minimize those impacts. These could be applied on a local scale, say within Etosha National Park, or at a country level, enlarging the geographic scale of the targeted area and/ or number of birds of interest. The movements performed by some of the birds across multiple borders could also put a strong case for the implementation of transnational conservation actions. As one last example, the

locations and estimated probabilities of finding vultures could also be integrated in risk assessment maps [35] to update or tailor actions to an area or species of interest.

Understandably, the synergies between the outputs and capabilities of the analysis presented in this thesis, and the desired conservation "crosscutting actions" would need to be addressed according to the aims of such actions.

6.3 Future work

One substantial feature of the work carried out in this thesis was the large volume of data analysed. This presented both computational and personal challenges. The methodological approach taken here was based on recently developed and statistically robust modelling principles. All the analyses conducted were centred on the individual, i.e., a description of the metrics was presented for each vulture separately. Additionally, in **Chapters 4** and **5** analysis was also based on a monthly time scale. Code for analysis was prepared and then executed separately for all birds. The results were inspected for ill-fitting issues but reassuringly no concerning faults were identified. Nonetheless improvements can always be found in order to best tailor each model to each bird. For example, the flexibility allowed on the smooth terms for the environmental covariates could be permitted to increase up to differing limits across individuals, and the number of allocated knots per bird-month could have also been higher in the bivariate smooths to allow a finer resolution of the often very large geographic areas. Nonetheless, these refinements all come at a cost. No significant issues were identified with the results shown here and these aspects would greatly increase the computational time of the models. Potentially higher smooth term flexibility might also make interpretation of the results more difficult. These improvements may be worth implementing if future analysis focus on a smaller geographic area, like the National Parks where the tag deployments took place, or more detailed analysis of a particular bird of interest (e.g., one of the *travellers* that will be at higher risk of exposure with human activities).

Another methodological step further would be to trial the integration with new approaches being made available that merge resource selection and step selection models for habitat preferences in animals [20]; such methods can incorporate information on movement and the environment at a step level (i.e., from one location to the consecutive).

One other big feature of the work presented here was the integrative approach taken. Information available on both the internal and external factors that unify the study of "movement ecology" [1] were sought to discuss the results. No other study before has presented such a detailed suite of findings describing the movement ecology of the study species. The study area within which the vultures displayed their movements (2,347,173 sq.km) was considerably larger than the areas where previous observations were generated (e.g. Etosha NP has 22,270 sq.km). This made the links between the movement patterns of vultures and its environment over time challenging. It could be for example that the environmental conditions in the northern section of the study area were different from the conditions in the southern section, for a given season. As such, there was potential for a mismatch of movement between systems inside the study area.

Another way the integrative approach took form involved the process of results interpretation. Metrics were presented individually (e.g., **Section 3.3.1**), they were discussed in combination with other relevant metrics (e.g., **Section 3.3.5**), figures displayed metrics jointly (e.g., **Figure 4-11**), and even displayed contrasted individuals to better illustrate the point being made (e.g., **Figure 5-2**). Future work could extend the joint interpretation of metrics, like modelling daily properties as a multivariate response.

But no doubt the one factor that was mentioned consistently in data interpretation was behaviour; the large variation found between birds was consistent across the metrics inspected supporting the concept that personality influences the way individuals perceive their surroundings, as they gather spatial information to build their "cognitive maps" [79]. Most of the satellite-based transmitters deployed in this study have an inbuilt accelerometer that records tri-axial movement information. Such detailed and directional movement can be used to infer behavioural states, with a growing body of literature being made available (e.g., [168, 169]).

Additionally, another relevant aspect to focus future attention on is the ground truthing of some aspects of the environment or the ecology of the study species. Namely, it would be of great relevance if birds could be approached once again to try and assess gender and breeding status. Much of the preceding studies relate their movement patterns to breeding and non-breeding individuals and the acquisition of such information for the vultures monitored in this study would allow better links to previous findings.

It would also be important to adjust the definition of "season". The analysis in this thesis were based on a definition centred in Etosha, an area that represents less than 1% of the study area. This may

have influenced the interpretation of results, namely in the figures where the background is coloured according to “season” irrespective of the geographic locations of the data being shown. For example, in **Figure 3-9** the mean daily distance travelled (DDT) is shown for each individual through time; even though there was no information incorporated in the models about space, the figure is indeed displaying data for birds that were, at a similar point in time, in very distant geographical areas. Better ways to integrate “season” should be sought, or an index of geographic area could be used.

There is a large realm of possible applications some of the findings in this thesis could have for conservation and management actions. Some were expressed in the previous section (**Section 6.2**). One additional interest for future work is the integration of some of the findings with the detection of changes in animal distribution. Two density surfaces can be compared to identify increases or decreases in the probability of finding an animal at a given location. The two surfaces could be the home ranges and respective core areas, to inspect in more detail what distinguishes those two levels of high usage for a bird. It could be a comparison to assess the effectiveness of a conservation or mitigation action (before and after, or inside and outside). It could also be to assess potential changes of movement under a set of climatic scenarios. The methodology implemented throughout the thesis has been widely applied in this field (e.g., [170]).

Given the conservation drive of the present study, it would be valuable to implement some of these ideas. This may be made possible by contacting relevant parties in Southern Africa.

6.4 Conclusions

This thesis presented a thorough and integrative study of the movement ecology of seventeen African vultures. Fifteen white-backed vultures and two hooded vultures transmitted nearly 240 thousand high resolution geo-referenced locations recorded between March 2015 and November 2018. The method implemented throughout this thesis adequately captured the innate autocorrelation structure of the data. Thus, the results are both unbiased, accurate and realistic in their associated uncertainty (95% confidence intervals and Coefficient of Variation). This generated an unprecedented set of detailed statistically robust results on the movement ecology of the study species.

An initial inspection of the vulture locations revealed that immatures do not necessary fly farther than the adults, as suggested in the literature. Two adults and the sub-adult white-backed vultures visited locations farther than 1,000 km away from where they were first seen, up to a maximum of 1,628 km (in 188 days); these measures far exceed what has been reported. Temporal changes in daily properties were perceived within and between individual. The lack of an apparent pattern between birds was consistent throughout analysis, supporting individual personality plays a big role in shaping the movement of these vultures. Metrics were interpreted separately as well as jointly. This triggered the speculation that some of the vultures analysed may be *locals*, never flying too far from their central areas of activity; in contrast, *travellers* performed long trips, possible long-range forays that reflected an adaptive exploratory foraging strategy to exploit remote resources or to search breeding mates.

Another very interesting novel finding was that monthly home ranges can change dramatically through time although the respective core areas do not vary as much. The ratio of core area to home range did not vary greatly between birds and indicated birds explore their habitat in a clearly patchy manner. As in the previous metrics, the mean range estimates were smaller for the hooded vultures when compared with the white-backed vultures, but given the uncertainty about these estimates, no conclusive differentiation could be detected between species. The interpretation of the monthly range maps in light of the breeding season of white-backed vultures in Central Namibia generated the speculation that among the studied individuals there may be *floaters*, non-breeding adults known to other bird populations, that perform larger movements during the breeding season.

The study area was characterised using environmental covariates, which were also used to assess habitat preferences for each vulture. Covariates described habitat characteristics, climate variables, and human presence. In keeping with previous results, each vulture showed its particular relationship with the environment with no obvious similarities detected between individuals. Vultures showed varied range areas and those that stayed more local were also exposed to less variable conditions. These observations will be relevant in future studies that address scenarios under Climate Change. The vegetation index (NDVI), nearest distance to road and nearest distance to river were overall the most important covariates. Inside or out of protected areas was not deemed to be important for half the individuals. However, the importance of such areas was unquestionable at the individual level. The mean number of locations recorded inside a protected area per month was higher than 80% for seven birds (43.75%). Also, vultures utilised areas of neighbouring countries such as in the Kavango-Zambezi region supporting the importance of transboundary initiatives.

This study presented new and meaningful insights on poorly known species of high conservation status and generated meaningful outputs that can provide the basis for tailoring future conservation plans. The findings of this comprehensive study can also be used as a baseline for future studies of detailed movement.

7 References

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Appendix

Appendix I Motivation: what's been reported so far

Despite the considerable amount of literature available on the two study species, only four previous studies show movement tracks of the study species. Those maps differ, greatly owing to the resolution of the data analysed and the aims of each study. Given the small number, these are mentioned here and extracts of the maps (when available) are shown.

White-backed vulture

The Cape Vulture (*Gyps coprotheres*) has one colony in Namibia, located on the cliffs of the Waterberg Plateau [97]. Five adult males and one immature were captured and fitted with satellite-tracking devices (solar-powered Argos/GPS PTT-100 made by Microwave Telemetry), and one the breeding partner was identified as an African white-backed vulture (*Gyps africanus*). One map (**Figure I. 1**) was presented to describe a movement track that intersected Etosha National Park and other territory also visited by the vultures analysed in this thesis.

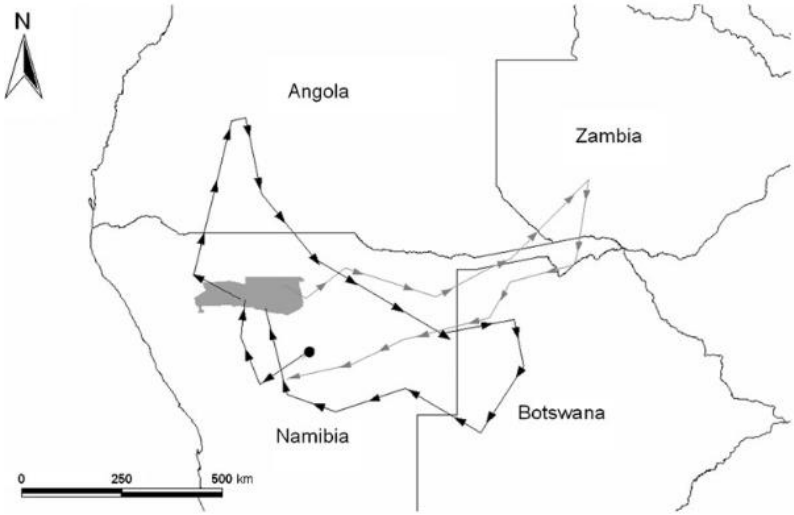

Figure I. 1 "Figure 1. Simplified path taken by one immature Cape Vulture (Imm1) between February 2005 and September 2005. The black dot shows the location of the Waterberg Plateau; the shaded area is Etosha National Park." Bamford *et al*., 2007 [97]

The sole preceding study that deployed satellite transmitters in vultures in Namibia focused on aspects of foraging efficiency. Several outputs were published [73, 76, 88]. One of such outputs compared long movements of three vulture species, from two distinct countries [73]. Eurasian griffon vultures (*Gyps fulvus*) were tracked in Israel and surrounding countries; 14 white-backed vultures and five lappet-faced vultures (Torgos tracheliotus), were monitored from Etosha National Park (Namibia). GPS-ACC transmitters were used (160 g; E-OBS, Munich, Germany). **Figure I. 2** was presented and shows joint kernel density estimation for all birds in each of the two study areas.

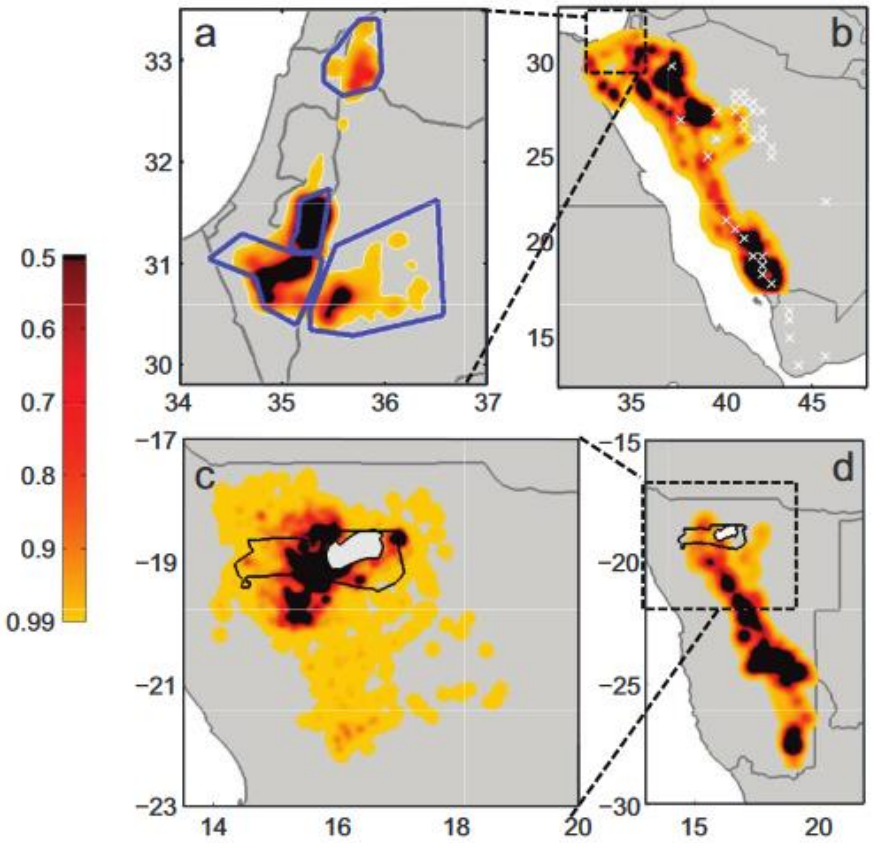

Figure I. 2 "Kernel density estimation for all Eurasian griffon vultures (EGVs) in Israel (a and b) and for all lappet-faced vultures and whitebacked vultures in Namibia (c and d). Color bars indicate increasing usage density, and X- and Y-axes show latitude and longitude, respectively, in degrees. Note the different spatial scales. Left panels (a, c) are for all non-long-range-foray (LRF) movements within home ranges, and right panels (b, d) are LRF movements. Blue polygons (a) indicate EGV subregions of activity, and white X symbols (b) indicate grid cell of known EGV colonies. The Etosha saltpan and the borders of Etosha National Park are shown by black polygons (c)." *Spiegel et al, 2015* [73]

Another publication displayed individual movement tracks from the white-backed vultures and lappet-faced vultures within Namibia (**Figure I. 3**) and highlighted contrasting movement patterns between those species [88].

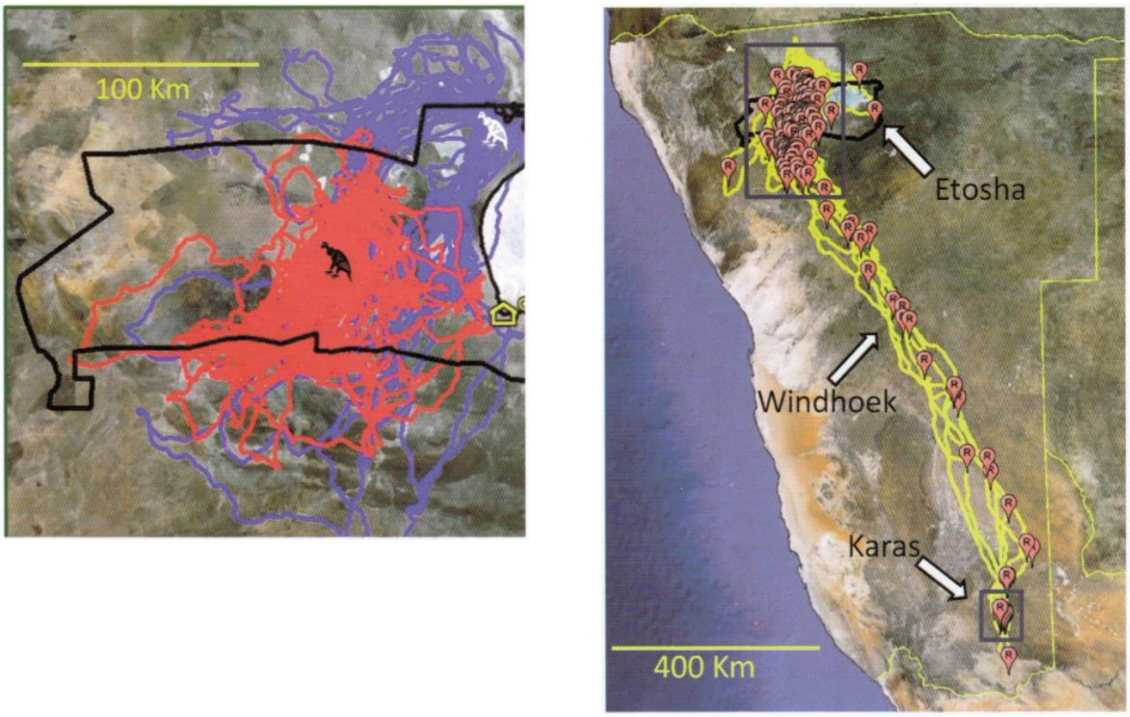

Figure I. 3 Left hand side: "Figure 1: GPS tracks of a white-backed vulture (WBV; blue line, Tag 95) and a lappet-faced vulture (LFV; red line, Tag 98). The tracks represent about six months worth of data (April – September 2008), and the vulture icons are the main roosting sites of these individuals during the tracking period. The thick black line is the boundary of Etosha National Park. It can be seen that both species routinely forage outside the park and that the LFV has a smaller home range."

Right hand side: "Figure 2: A GPS track of a lappet-faced vulture (E036) showing its long-range forays (LRFs). The yellow line is the track and red icons represent roosting sites. During most of 2009, E036 foraged in Etosha National Park and surroundings (upper black rectangle) areas. On three distinct occasions, E036 engaged in LRFs, with direct flight towards a very specific area east of Karasburg (smaller rectangle) where he stayed for a few days on each occasion." Spiegel *et al.*, 2013 [88].

Six immature African white-backed vultures were tracked in South Africa using GPS-GSM tracking units (Africa Wildlife Tracking Ltd., Pretoria, South Africa; www.awt.co.za) to assess their movement patterns, their use of protected areas as well as the time vultures spent in the vicinity of supplementary feeding sites [39]. Different methods to estimate range areas were contrasted, and maps presented (**Figure I. 4**). The map based on the more detailed grid method (top left hand side, **Figure I. 4**) showed some similarities with the vultures in this thesis that flew over Botswana.

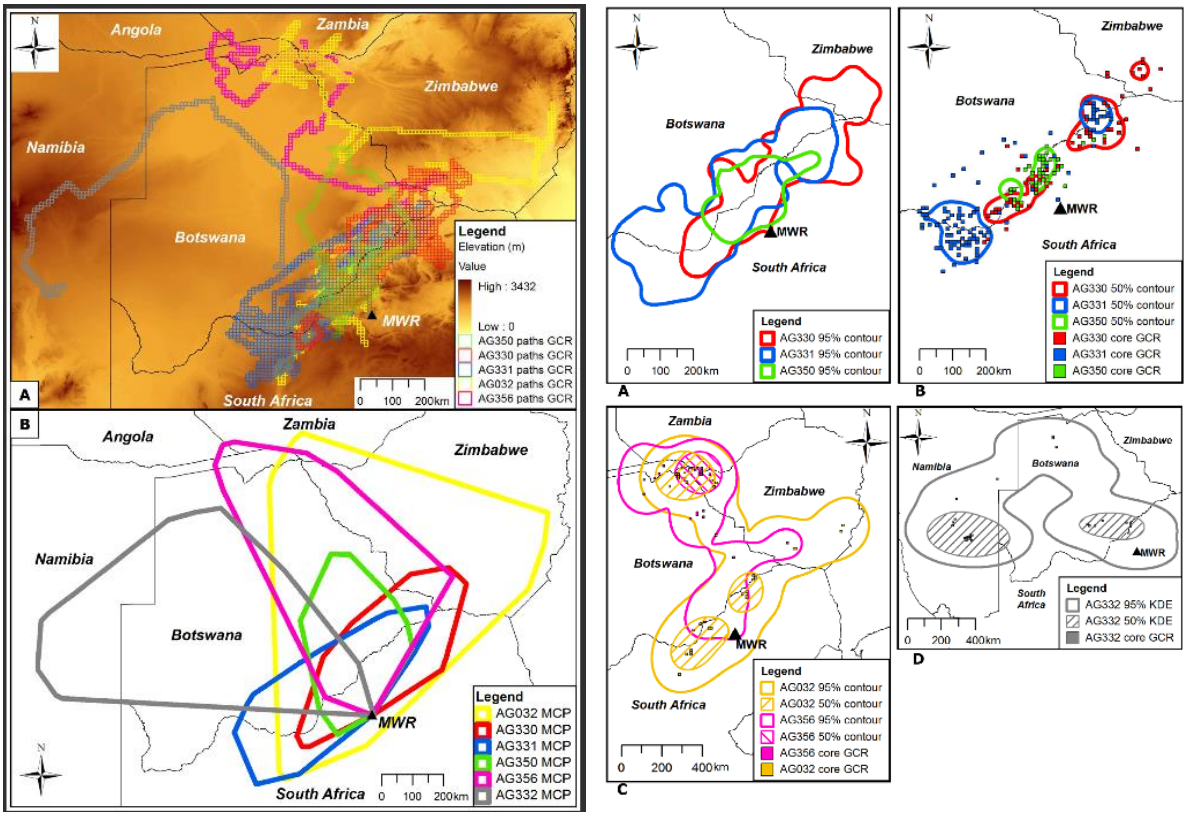

Figure I. 4 Left hand side: "Figure 1. Foraging ranges represented by (A) path GCRs and (B) MCPs for six immature African white-backed vultures. Path GCRs (A) represent 10610 km grid cells intersected by a continuous line between all consecutive GPS locations recorded during the total tracking period of each vulture. MCPs (B) were created by connecting the outermost GPS locations recorded for each vulture. Mankwe Wildlife Reserve capture site is indicated by a black triangle and ''MWR''. doi:10.1371/journal.pone.0052813.g001".

Right hand side: "Figure 2. Overall and core foraging ranges for each individual. 95% KDE contours represent overall foraging ranges, 50% KDE contours and core GCRs represent core foraging ranges. (A) and (B) show the foraging ranges for AG330, AG331 and AG350; (C) shows the foraging ranges for AG032 and AG356; (D) shows the foraging ranges for AG332. Mankwe Wildlife Reserve capture site is indicated by a black triangle and ''MWR''. doi:10.1371/journal.pone.0052813.g002". Phipps *et al*, 2013 [39]

Hooded vulture

Reading *et al.* (2018) provide the only published work on home range size and movement patterns of hooded vultures (*Necrosyrtes monachus*) in southern Africa, and as such is worth the inclusion in this section [98]. Even though the authors discuss estimates between age and sex groups, as well as temporal changes, the work presents no maps to assess spatial similarities with the hooded vultures monitored in this thesis.

Appendix II Distribution maps for each vulture

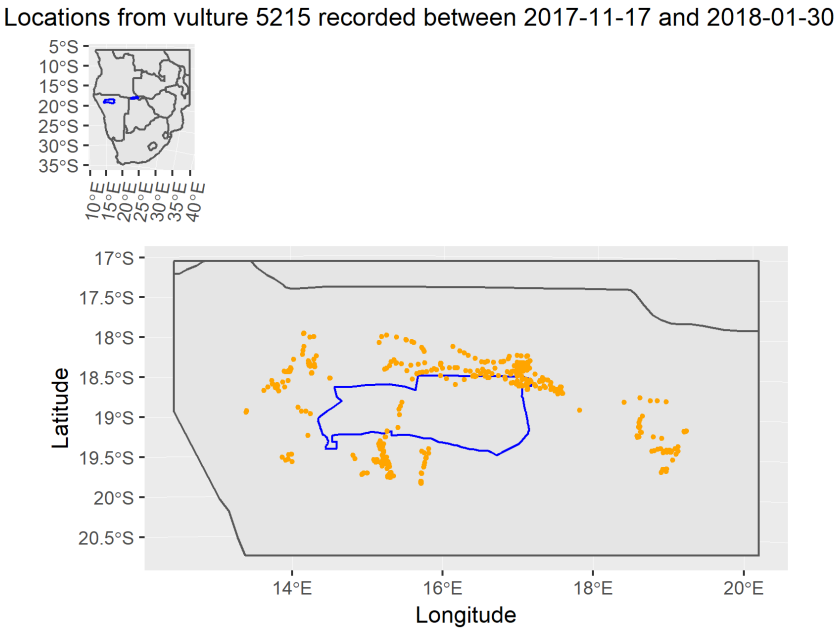

Figure II. 1 Geographic extent of movements for bird ID 5215 obtained from the satellite transmitters during this study.

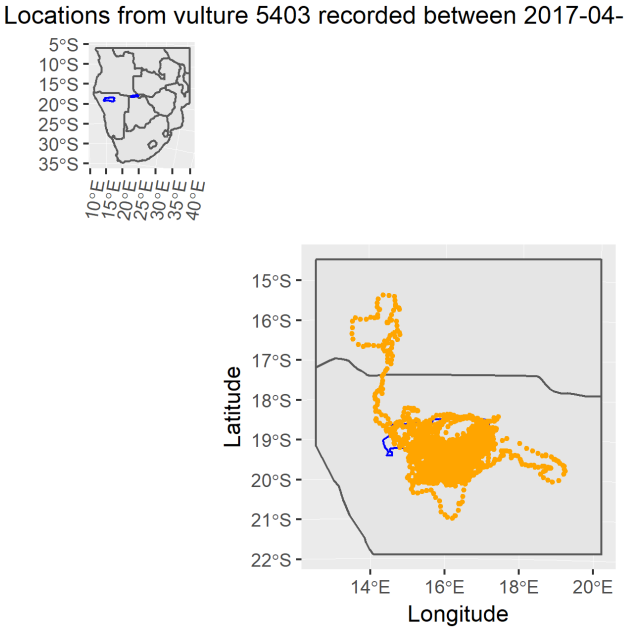

Figure II. 2 Geographic extent of movements for bird ID 5403 obtained from the satellite transmitters during this study.

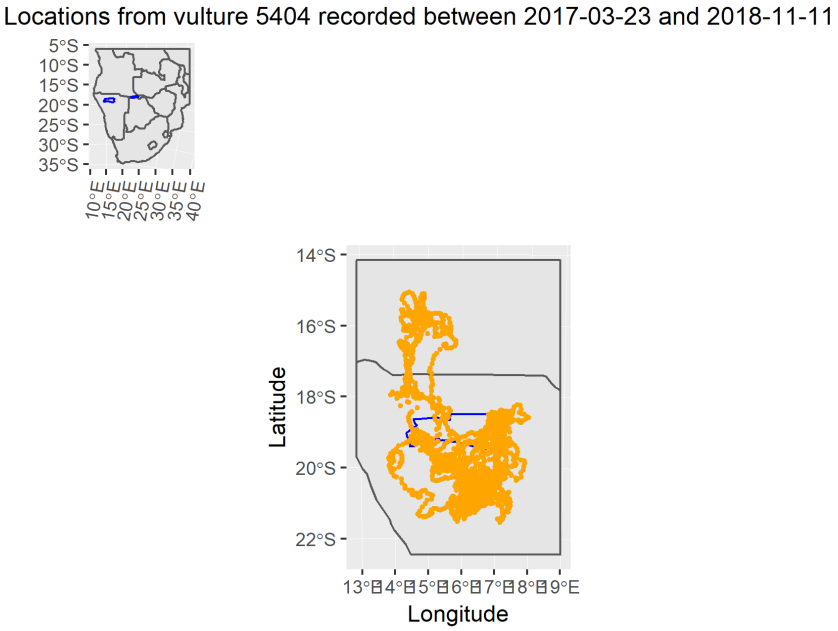

Figure II. 3 Geographic extent of movements for bird ID 5404 obtained from the satellite transmitters during this study.

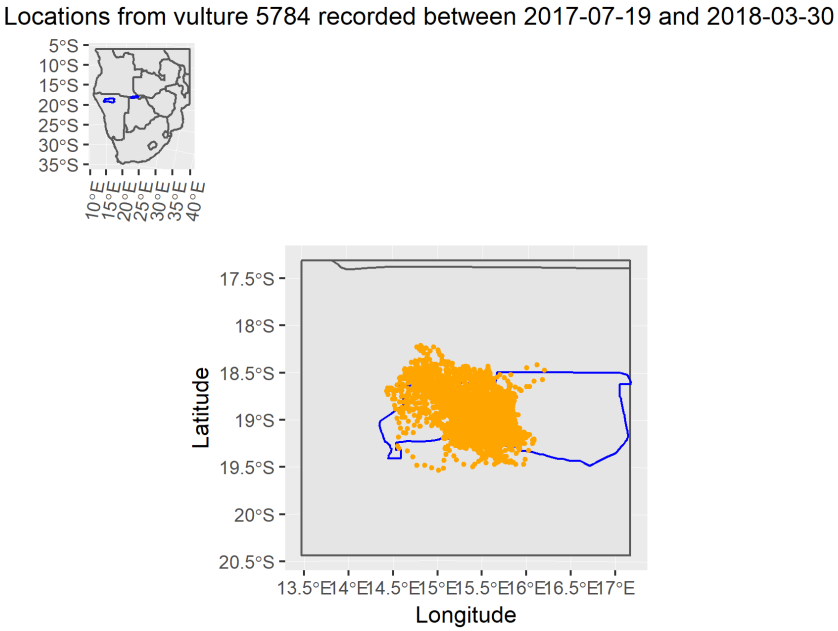

Figure II. 4 Geographic extent of movements for bird ID 5784 obtained from the satellite transmitters during this study.

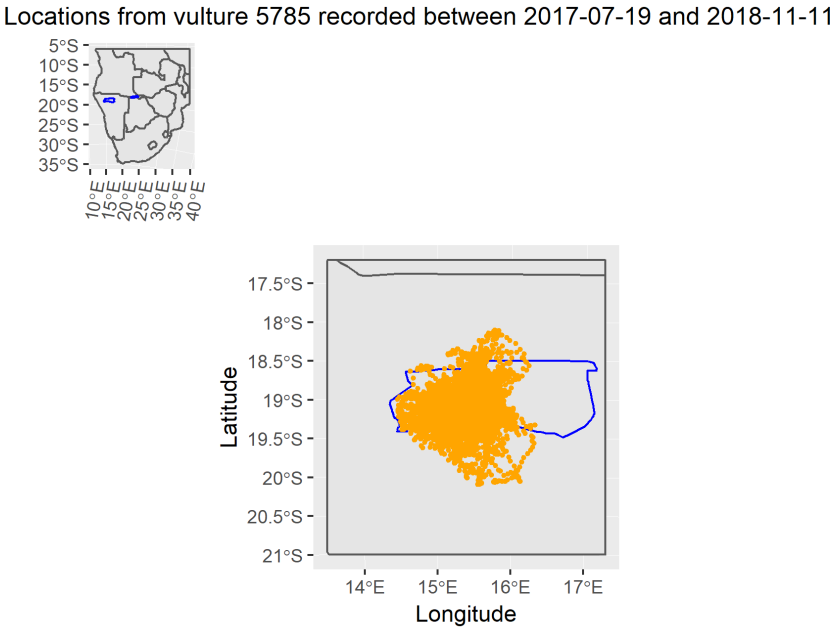

Figure II. 5 Geographic extent of movements for bird ID 5785 obtained from the satellite transmitters during this study.

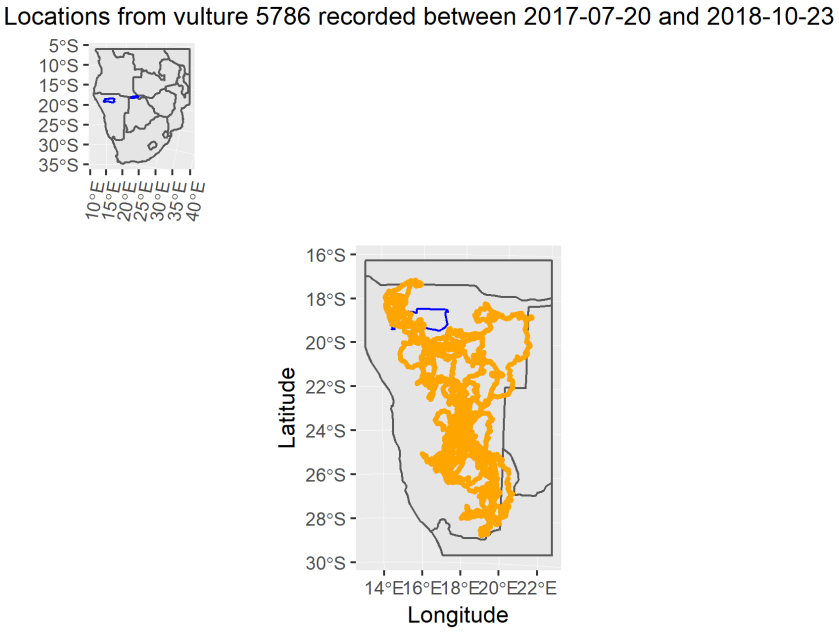

Figure II. 6 Geographic extent of movements for bird ID 5786 obtained from the satellite transmitters during this study.

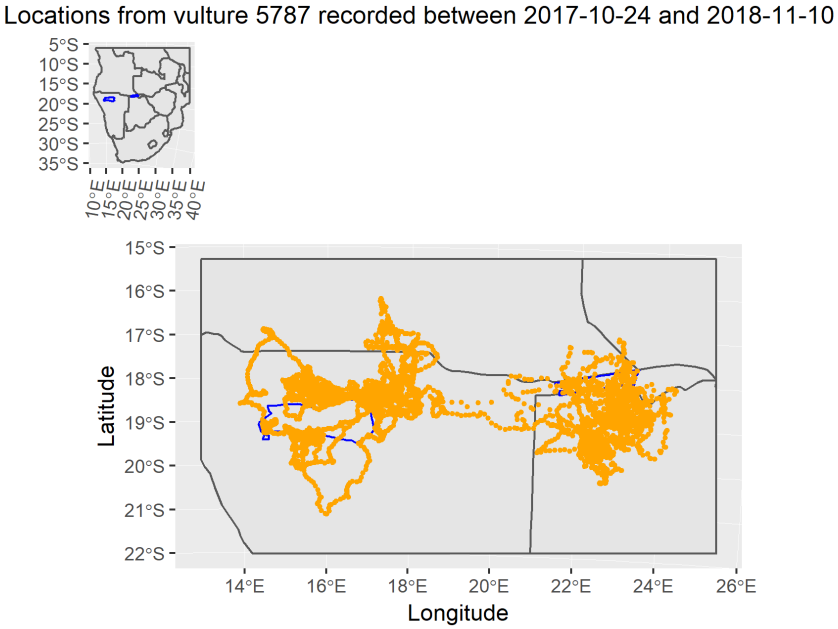

Figure II. 7 Geographic extent of movements for bird ID 5787 obtained from the satellite transmitters during this study.

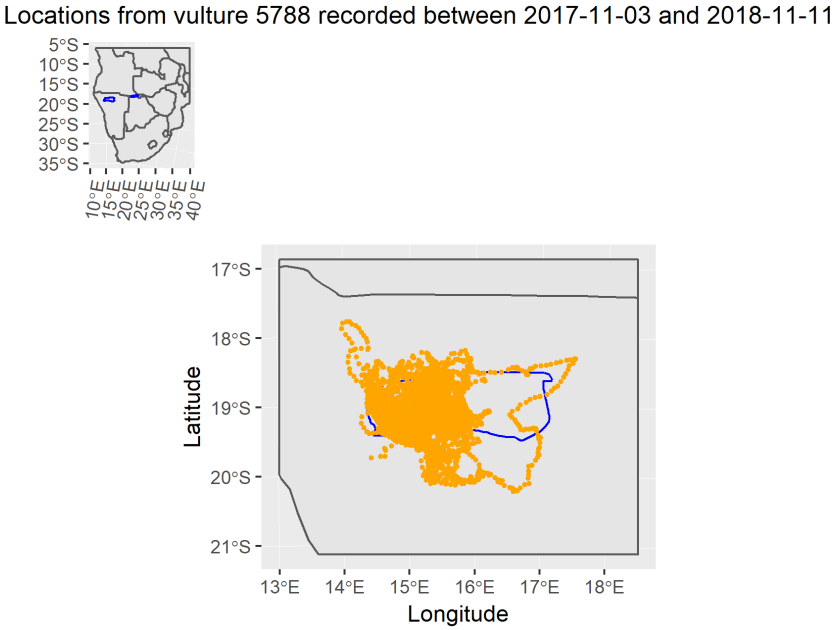

Figure II. 8 Geographic extent of movements for bird ID 5788 obtained from the satellite transmitters during this study.

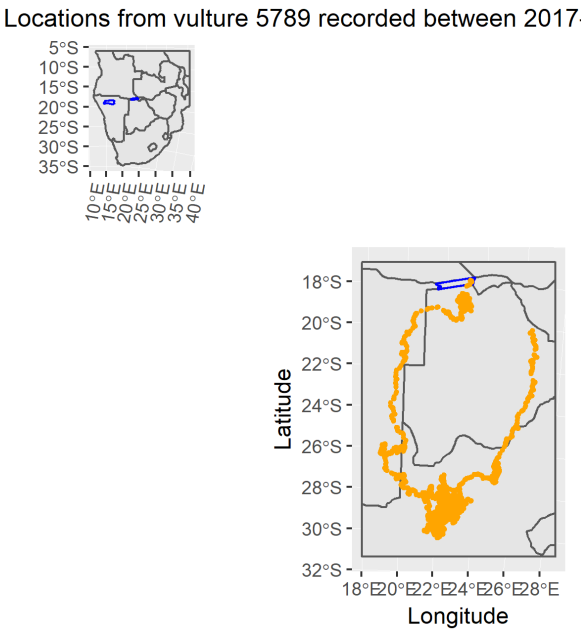

Figure II. 9 Geographic extent of movements for bird ID 5789 obtained from the satellite transmitters during this study.

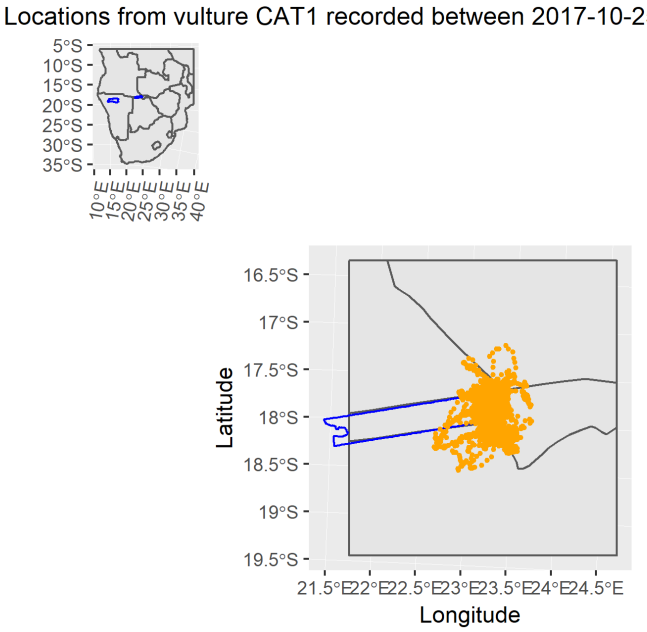

Figure II. 10 Geographic extent of movements for bird ID CAT1 obtained from the satellite transmitters during this study.

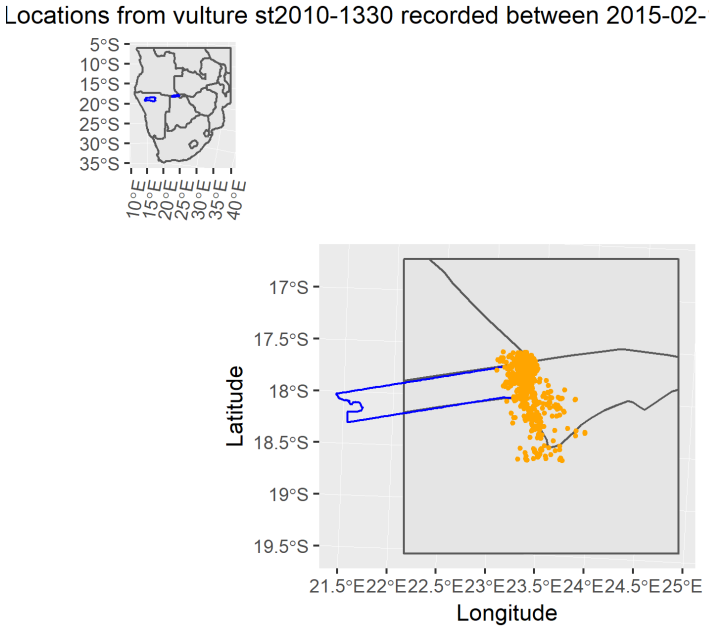

Figure II. 11 Geographic extent of movements for bird ID st2010-1330 obtained from the satellite transmitters during this study.

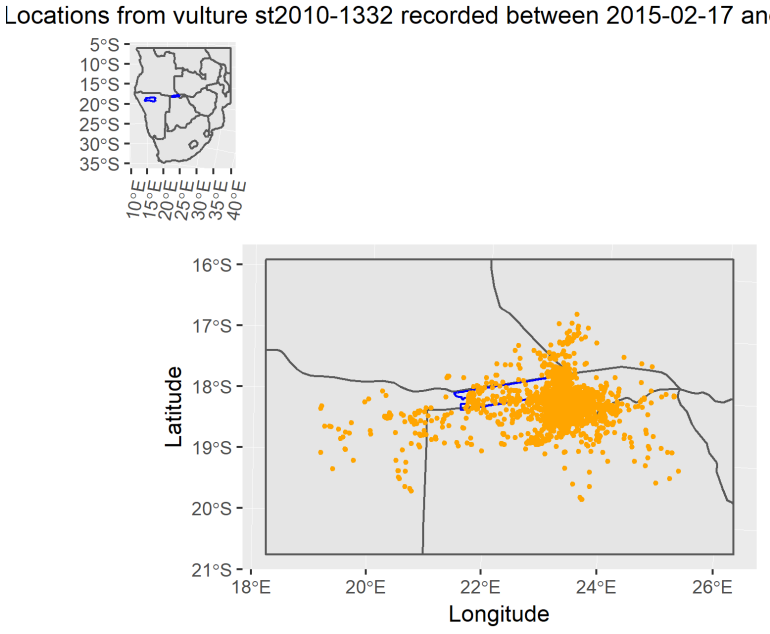

Figure II. 12 Geographic extent of movements for bird ID st2010-1332 obtained from the satellite transmitters during this study.

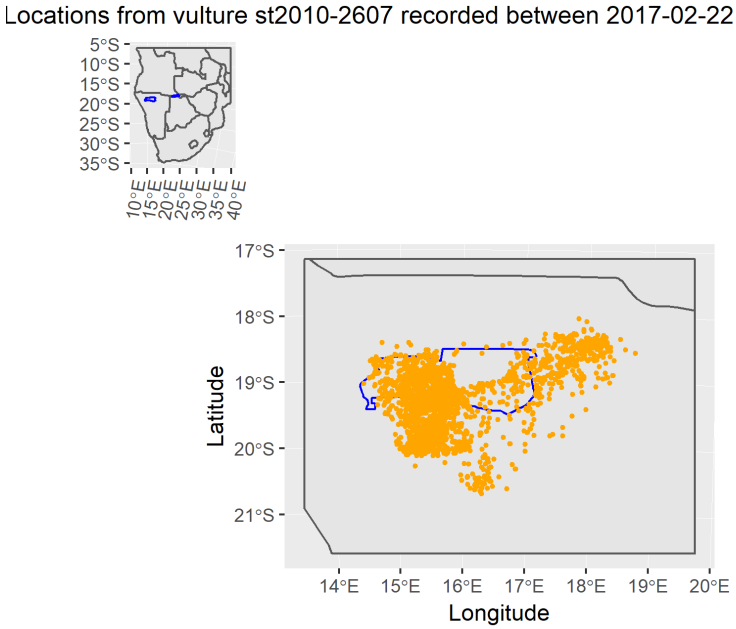

Figure II. 13 Geographic extent of movements for bird ID st2010-2607 obtained from the satellite transmitters during this study.

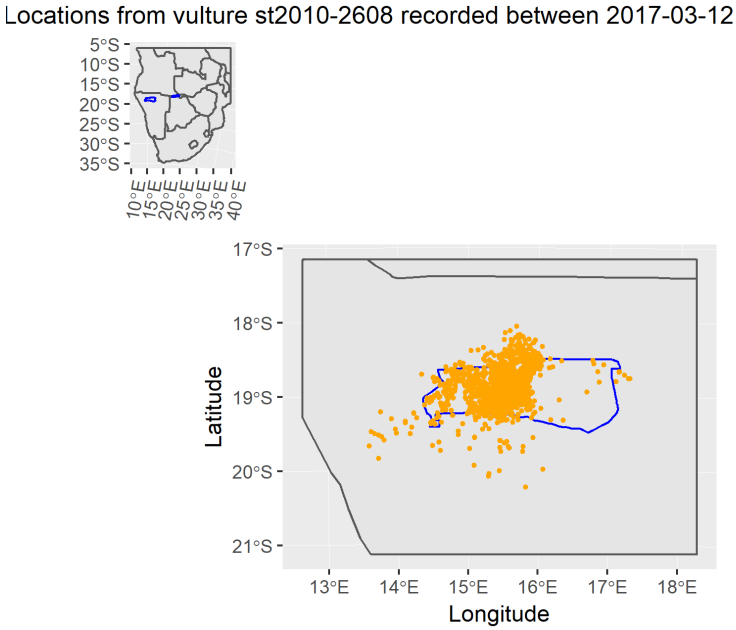

Figure II. 14 Geographic extent of movements for bird ID st2010-2608 obtained from the satellite transmitters during this study.

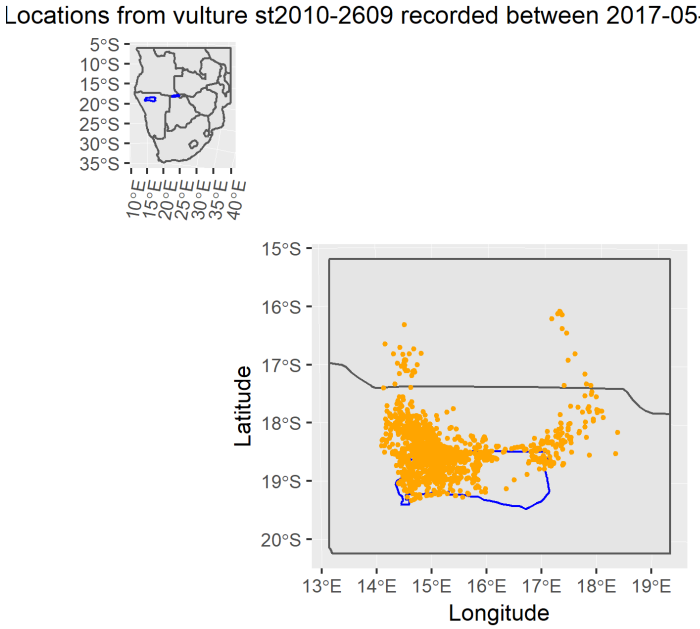

Figure II. 15 Geographic extent of movements for bird ID st2010-2609 obtained from the satellite transmitters during this study.

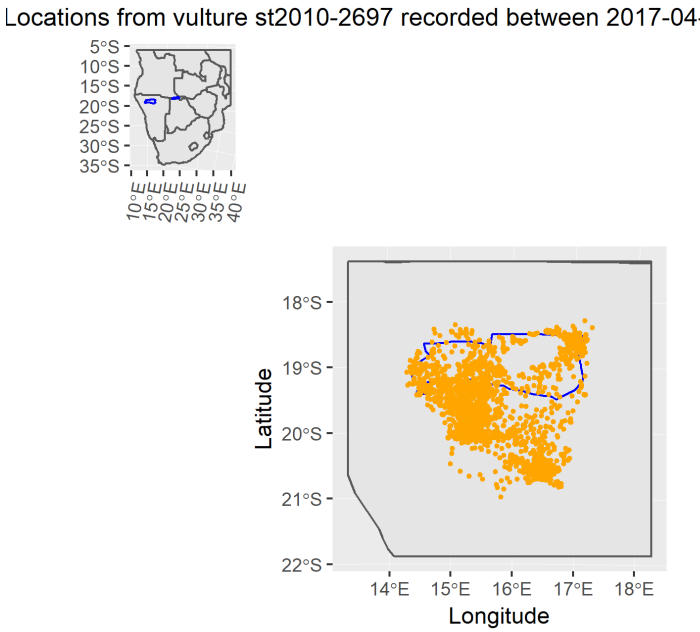

Figure II. 16 Geographic extent of movements for bird ID st2010-2697 obtained from the satellite transmitters during this study.

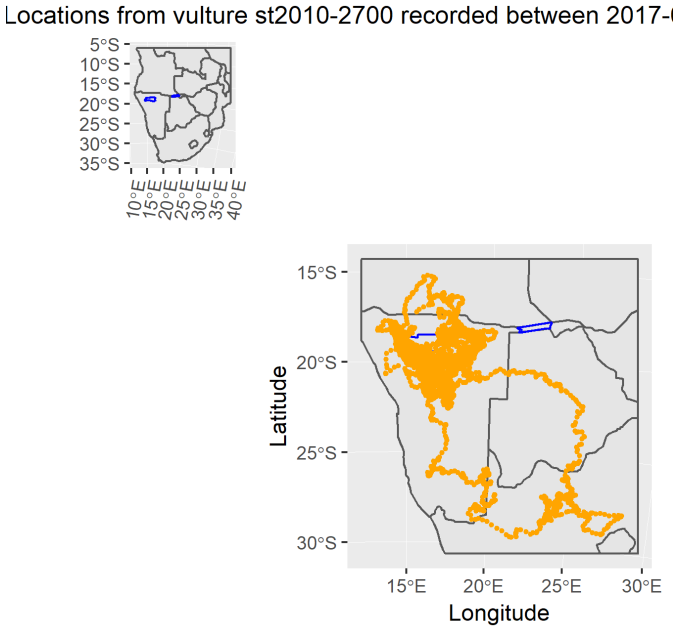

Figure II. 17 Geographic extent of movements for bird ID st2010-2700 obtained from the satellite transmitters during this study.

Appendix III Daily movement properties: farther data and modelling details

Data summary

Table III. 1 Summary of the properties of daily movement patterns per individual. Mean, 95% confidence intervals (inside square brackets) and range (inside round brackets) are show. Distances as follow: daily distance travelled (DDT), daily overall displacement (DOD), daily maximum displacement (DMD), straightness of a daily path (SDP). The total number of days analysed per individual is also shown. Immature and sub-adult vultures are highlighted in bold.

Species and tag ID	Number of days	DDT (km)	DOD (km)	DMD (km)	SDP
White-backed vultures					
5215	59	50.15 [0.06;217.7] (0.04-235.97)	32.89 [0.02;196.31] (0.01-206.44)	35.71 [0.02;197.46] (0.02-206.44)	0.78 [0.38;1.0] (0.34-1.0)
5403	347	85.94 [0.39;239.99] (0.01-337.64)	48.91 [0.01;168.27] (0-215.92)	54.39 [0.15;172.32] (0.01-223.49)	0.72 [0.31;0.97] (0.06-0.99)
5404	537	87.89 [0.68;215.13] (0.01-275.38)	31.51 [0.05;126.76] (0-197.05)	39.91 [0.19;128.97] (0.01-197.24)	0.63 [0.27;0.97] (0.15-1.0)
5784	255	162.71 [32.66;317.4] (0.31-357.45)	34.45 [0;117.62] (0-148.75)	51.23 [8.12;129.92] (0.02-148.75)	0.52 [0.17;0.91] (0.06-0.98)
5785	406	134.25 [0.25;312.3] (0.06-416.08)	45.98 [0;111.64] (0-142.96)	57.68 [0.01;126.68] (0.01-144.62)	0.6 [0.1;0.94] (0.06-1.0)
5786	413	101.75 [1.33;283.31] (0.01-429.17)	45.55 [0.01;181.95] (0-224.25)	53.43 [0.43;185.76] (0-225.29)	0.65 [0.3;0.94] (0.18-1.0)
5787	322	89.99 [1.1;263.97] (0.31-393.65)	39.91 [0.04;171.32] (0-357.65)	46.43 [0.23;184.12] (0.03-358.52)	0.63 [0.24;0.94] (0.14-0.97)
5788	227	117.56 [2.25;276.3] (0.06-345.18)	46.81 [0.08;138.06] (0-220.69)	57.33 [0.62;141.09] (0.01-220.71)	0.68 [0.3;0.99] (0.09-1.0)
5789	143	120.41 [3.56;283.22] (1.5-355.37)	46.63 [0.27;198.42] (0-310.73)	59.64 [1.47;204.15] (0.62-311.74)	0.68 [0.33;0.93] (0.21-0.98)
st2010-1332	929	68.85 [0.76;186.03] (0.02-257.44)	30.57 [0.03;127.72] (0-215.8)	38.41 [0.29;129.41] (0.02-215.8)	0.76 [0.31;1.0] (0.2-1.0)
st2010-2607	560	88.98 [0.38;237.28] (0.05-385.15)	51.41 [0.02;193.41] (0-310.8)	58.74 [0.25;193.41] (0.01-310.8)	0.80 [0.38;1.0] (0.22-1.0)
st2010-2608	436	104.76 [0.32;219.24] (0.04-331.13)	32.76 [0.01;114.58] (0-171.29)	48.31 [0.2;119.73] (0.01-171.29)	0.72 [0.29;1.0] (0.24-1.0)
st2010-2609	320	105.16 [0.35;232.2] (0.23-313.53)	45.50 [0;170.28] (0-256.86)	57.57 [0.05;170.28] (0.02-260.41)	0.72 [0.29;0.99] (0.11-1.0)
st2010-2697	445	70.73 [0.55;204.69] (0.21-268.37)	35.29 [0.15;147.71] (0-214.09)	41.15 [0.31;147.74] (0.03-217.13)	0.73 [0.34;1.0] (0.16-1.0)
st2010-2700	465	78.01 [0.37;223.32] (0.23-279.54)	42.5 [0.03;172.79] (0-221.31)	47.67 [0.08;172.88] (0.03-221.31)	0.71 [0.3;0.99] (0.15-1.0)
Hooded vultures					
CAT1	316	68.88 [1.01;179.03] (0.42-229.78)	17.46 [0.01;70.31] (0-94.2)	26.52 [0.12;76.77] (0.02-102.1)	0.61 [0.18;0.92] (0.05-0.97)
st2010-1330	424	29.72 [0.46;98.02] (0.22-148.97)	11.33 [0.02;59.56] (0-108.06)	15.8 [0.15;60.77] (0.06-108.45)	0.73 [0.26;1.0] (0.17-1.0)

Modelling daily distance travelled (DDT)

Model selection

Table III. 2 Summary of the performance of the models tested for daily distance travelled (DDT). The model covariates are shown as well as the respective number of parameters (k), results from 10-fold cross validation bootstraps (mean, lower and upper confidence intervals), Akaike and Bayesian information criteria (AIC, BIC). Scores are shown as the difference from the lowest score. In bold are highlighted the best performance scores.

Model	k	Cvmean	Cvlower	Cvupper	AIC	BIC	Δ AIC	Δ BIC
Year : Month	44	4437.466	4423.1	4456.432	74105.64	74411.42	1291.64	722.84
Year : Season	12	4487.514	4479.705	4496.436	74223.01	74311.35	1409.01	622.77
Tag	17	4080.943	4069.776	4095.207	73566.27	**73688.58**	752.27	**0**
Tag : Year : Month	248	**3845.806**	3800.512	3889.124	**72814**	74505.95	**0**	817.37
Tag : Year : Season	78	3929.838	3911.992	3961.318	73224.09	73760.89	410.09	72.31

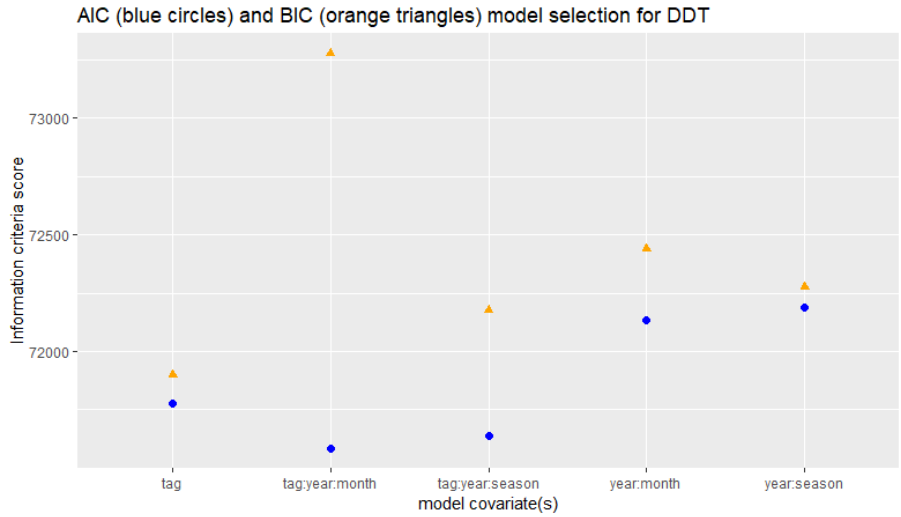

Figure III. 1 Performance of the models tested for daily distance travelled (DDT) using the Akaike (AIC, shown in blue circles) and Bayesian information criteria (BIC, shown in orange triangles).

Model results

Table III. 3 Summary of the predictions generated by the best candidate model for daily distance travelled (DDT), for each of birds analysed. The minima (min.) and maxima (max.) mean predictions with respective upper and lower confidence intervals (CI) shown for DDT. The respective time when those predictions were expected to occur are also shown: Ymo – year-month, Se – season. Seasons: hot wet (1hw) - January to May, cold dry (2cd) - June to August, small rain (2sr) – September to December. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	no. months	min mean DDT	min lower CI	min upper CI	min Ymo	min Se	max mean DDT	max lower CI	max upper CI	max Ymo	max Se	Deployment area
5215	3	28.94	12.37	53.89	201801	1hw	73.29	47.48	110.73	201711	3sr	Etosha NP
5403	13	4.08	4.08	4.08	201805	1hw	120.74	90.43	160.70	201711	3sr	Etosha NP
5404	19	44.23	29.77	61.25	201803	1hw	126.15	100.73	157.08	201703	1hw	Kunene Region
5784	9	127.51	95.41	160.57	201803	1hw	195.59	152.07	242.33	201711	3sr	Etosha NP
5785	14	73.54	53.49	100.19	201806	2cd	220.27	167.30	284.35	201712	3sr	Etosha NP
5786	15	4.90	0.47	18.21	201809	3sr	149.62	130.67	167.71	201711	3sr	Etosha NP
5787	12	39.57	27.58	54.09	201802	1hw	176.36	160.20	192.81	201808	2cd	Bwabwata NP
5788	10	32.90	32.28	33.54	201806	2cd	188.36	150.05	233.42	201711	3sr	Etosha NP
5789	6	98.63	80.21	120.68	201712	3sr	154.27	115.77	195.03	201711	3sr	Bwabwata NP
CAT1	12	57.43	49.13	65.37	201806	2cd	88.26	58.48	126.79	201809	3sr	Bwabwata NP
st2010-1330	15	14.79	10.91	19.08	201505	1hw	42.49	24.99	72.18	201604	1hw	Bwabwata NP
st2010-1332	38	34.42	34.42	34.42	201802	1hw	108.77	85.76	133.44	201510	3sr	Bwabwata NP
st2010-2607	20	33.79	21.33	49.16	201702	1hw	135.35	103.08	177.71	201711	3sr	Etosha NP
st2010-2608	17	17.27	6.02	37.68	201807	2cd	134.39	119.95	149.43	201801	1hw	Etosha NP
st2010-2609	12	78.80	68.01	91.17	201803	1hw	150.88	123.47	182.46	201710	3sr	Etosha NP
st2010-2697	16	34.47	24.36	46.86	201803	1hw	109.51	87.77	133.92	201711	3sr	Etosha NP
st2010-2700	17	46.13	32.59	63.17	201807	2cd	125.04	103.55	146.27	201708	2cd	Etosha NP

Modelling daily overall displacement (DOD)

Model selection

Table III. 4 Summary of the performance of the models tested for daily overall displacement (DOD). The model covariates are shown as well as the respective number of parameters (k), results from 10-fold cross validation bootstraps (mean, lower and upper confidence intervals), Akaike and Bayesian information criteria (AIC, BIC). Scores are shown as the difference from the lowest score. In bold are highlighted the best performance scores. Three of the models did not converge and as such no selection scores are available (marked as NA).

Model	k	Cvmean	Cvlower	Cvupper	AIC	BIC	Δ AIC	Δ BIC
Year x Month	44	NA	NA	NA	NA	NA	NA	NA
Year x Season	12	1681.612	1679.04	1684.826	57885.87	57974.2	200.81	166.83
Tag	17	**1636.16**	1632.913	1640.283	**57685.06**	**57807.37**	0	0
Tag x Year x Month	248	NA	NA	NA	NA	NA	NA	NA
Tag x Year x Season	78	NA	NA	NA	NA	NA	NA	NA

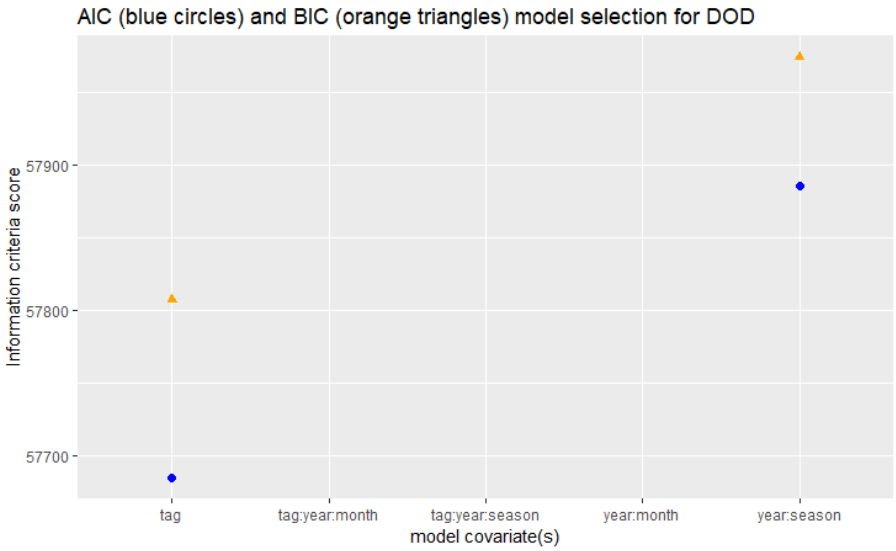

Figure III. 2 Performance of the models tested for daily overall displacement (DOD) using the Akaike (AIC, shown in blue circles) and Bayesian information criteria (BIC, shown in orange triangles). Three of the models did not converge and as such no selection scores are available.

Best model assessment

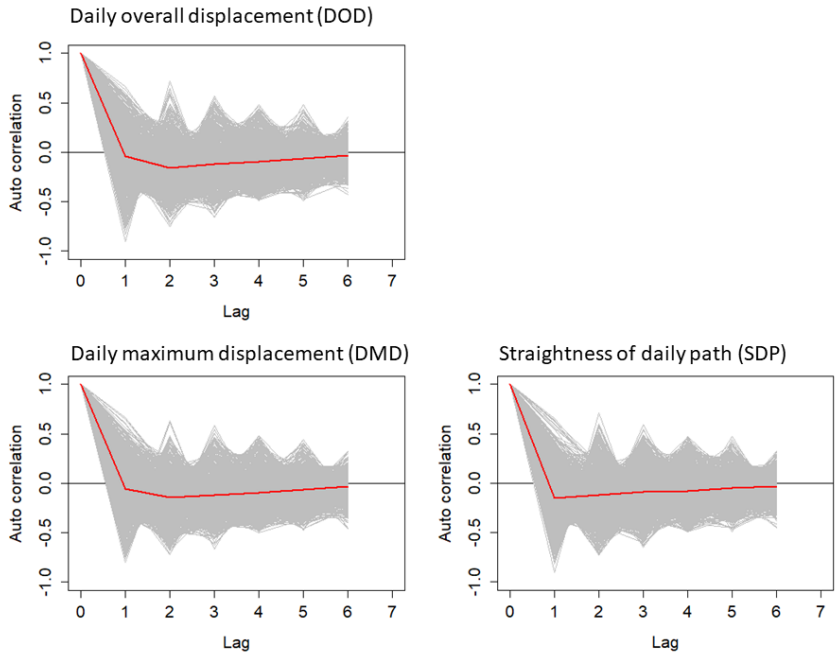

Figure III. 3 Visual assessment on the independence of model residuals for three daily properties (DOD, DMD and SDP, anti-clockwise), via the autocorrelation function plots.

Model results

Table III. 5 Summary of the predictions generated by the best candidate model for daily overall displacement (DOD), for each of birds analysed, with respective upper and lower confidence intervals (CI). Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	no obs.	mean DOD	lower CI	upper CI	Deployment area
5215	59	34.20	22.42	52.42	Etosha NP
5403	346	49.07	43.67	55.20	Etosha NP
5404	537	31.65	27.58	35.77	Kunene Region
5784	255	34.63	28.56	41.97	Etosha NP
5785	405	46.08	41.91	50.37	Etosha NP
5786	413	45.89	39.24	54.61	Etosha NP
5787	322	40.19	31.89	49.62	Bwabwata NP
5788	226	46.84	40.41	53.72	Etosha NP
5789	143	47.16	34.28	62.92	Bwabwata NP
CAT1	316	17.51	14.48	21.14	Bwabwata NP
st2010-1330	424	11.42	9.15	14.24	Bwabwata NP
st2010-1332	929	30.67	27.65	33.99	Bwabwata NP
st2010-2607	560	51.61	46.28	57.28	Etosha NP
st2010-2608	436	32.91	28.82	36.97	Etosha NP
st2010-2609	320	45.53	38.09	53.44	Etosha NP
st2010-2697	445	35.38	31.15	39.64	Etosha NP
st2010-2700	465	42.81	37.01	49.93	Etosha NP

Modelling daily maximum displacement (DMD)

Model selection

Table III. 6 Summary of the performance of the models tested for daily maximum displacement (DMD). The model covariates are shown as well as the respective number of parameters (k), results from 10-fold cross validation bootstraps (mean, lower and upper confidence intervals), Akaike and Bayesian information criteria (AIC, BIC). Scores are shown as the difference from the lowest score. In bold are highlighted the best performance scores.

Model	k	Cvmean	Cvlower	Cvupper	AIC	BIC	Δ AIC	Δ BIC
Year : Month	44	1603.556	1598.108	1611.818	67380.17	67685.94	651.50	382.90
Year : Season	12	1600.23	1597.606	1603.506	67415.76	67504.09	687.09	201.05
Tag	17	1549.006	1545.149	1553.045	67180.73	**67303.04**	452.06	**0**
Tag : Year : Month	248	1522.247	1504.082	1542.277	**66728.67**	68420.62	**0**	1117.58
Tag : Year : Season	78	**1514.184**	1503.62	1521.712	66940.61	67477.41	211.94	174.37

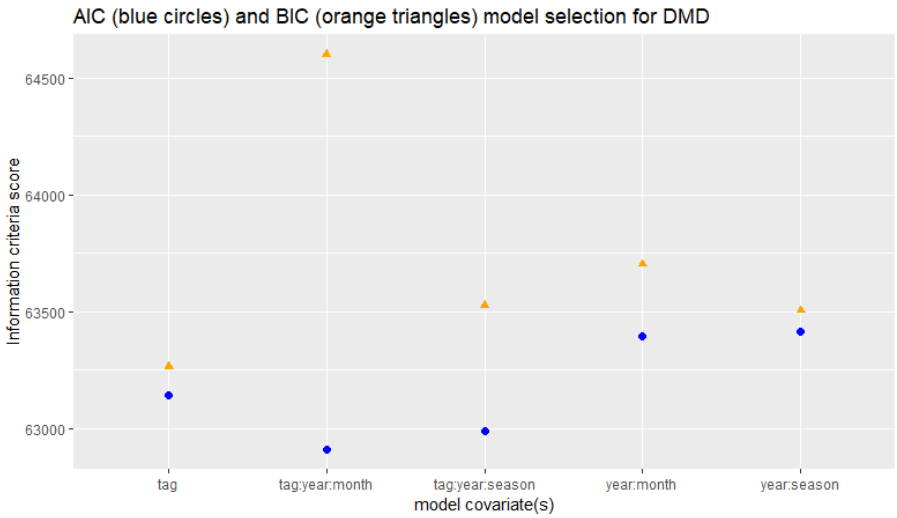

Figure III. 4 Performance of the models tested for daily maximum displacement (DMD) using the Akaike (AIC, shown in blue circles) and Bayesian information criteria (BIC, shown in orange triangles).

Best model assessment

See **Figure III. 3** above.

Model results

Table III. 7 Summary of the predictions generated by the best candidate model for daily maximum displacement (DMD), for each of birds analysed. The minima (min.) and maxima (max.) mean predictions with respective upper and lower confidence intervals (CI) shown for DMD. The respective time when those predictions were expected to occur are also shown: Yse – year-season, Se – season. Seasons: hot wet (1hw) - January to May, cold dry (2cd) - June to August, small rain (2sr) – September to December. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	no. seasons	min mean DMD	min lower CI	min upper CI	min Yse	min Se	max mean	max lower CI	max upper CI	max Yse	max Se	Deployment area
5215	2	18.03	8.34	33.35	20181hw	1hw	48.43	32.85	67.28	20173sr	3sr	Etosha NP
5403	4	41.77	33.98	49.48	20171hw	1hw	65.35	54.75	77.40	20173sr	3sr	Etosha NP
5404	6	27.67	22.57	33.61	20181hw	1hw	53.10	41.37	67.60	20172cd	2cd	Kunene Region
5784	3	40.99	33.99	49.40	20181hw	1hw	59.75	54.12	65.57	20172cd	2cd	Etosha NP
5785	4	48.21	42.01	54.74	20182cd	2cd	70.77	61.11	81.37	20172cd	2cd	Etosha NP
5786	5	3.96	0.39	15.12	20183sr	3sr	65.68	52.43	81.74	20173sr	3sr	Etosha NP
5787	4	27.45	20.33	35.11	20181hw	1hw	87.81	69.25	110.57	20183sr	3sr	Bwabwata NP
5788	4	50.74	40.91	62.41	20181hw	1hw	67.35	56.28	78.68	20173sr	3sr	Etosha NP
5789	2	59.11	48.14	72.23	20181hw	1hw	61.59	43.29	86.76	20173sr	3sr	Bwabwata NP
CAT1	4	24.72	19.67	30.23	20182cd	2cd	33.47	21.26	49.57	20183sr	3sr	Bwabwata NP
st2010-1330	4	11.21	6.80	16.89	20151hw	1hw	19.02	15.18	23.50	20161hw	1hw	Bwabwata NP
st2010-1332	10	26.18	22.26	31.11	20163sr	3sr	55.57	45.80	66.10	20153sr	3sr	Bwabwata NP
st2010-2607	6	24.30	23.09	25.49	20183sr	3sr	76.01	61.71	92.15	20171hw	1hw	Etosha NP
st2010-2608	5	40.22	21.48	66.70	20182cd	2cd	57.75	50.05	66.11	20172cd	2cd	Etosha NP
st2010-2609	4	46.52	40.32	52.96	20181hw	1hw	69.99	58.35	85.14	20173sr	3sr	Etosha NP
st2010-2697	5	35.89	28.00	46.00	20172cd	2cd	50.08	43.02	57.66	20182cd	2cd	Etosha NP
st2010-2700	6	30.93	19.75	46.69	20183sr	3sr	63.50	50.74	78.18	20173sr	3sr	Etosha NP

Modelling straightness of a daily path (SPD)

Model selection

Table III. 8 Summary of the performance of the models tested for straightness of a daily path (SPD). The model covariates are shown as well as the respective number of parameters (k), results from 10-fold cross validation bootstraps (mean, lower and upper confidence intervals), Akaike and Bayesian information criteria (AIC, BIC). Scores are shown as the difference from the lowest score. In bold are highlighted the best performance scores.

Model	k	Cvmean	Cvlower	Cvupper	AIC	BIC	Δ AIC	Δ BIC
Year : Month	44	0.04584243	0.04571328	0.04601974	-3822.73	-3516.956	685.24	868.71
Year : Season	12	0.0454959	0.04544406	0.04555923	-3822.081	-3733.746	685.89	651.92
Tag	17	**0.04200238**	0.04195494	0.04206534	**-4507.971**	**-4385.662**	**0**	**0**
Tag : Year : Month	248	0.04317811	0.04292728	0.04339272	-4459.867	-2767.918	48.10	1617.74
Tag : Year : Season	78	0.0421488	0.04202688	0.04230995	-4507.656	-3970.852	0.315	414.81

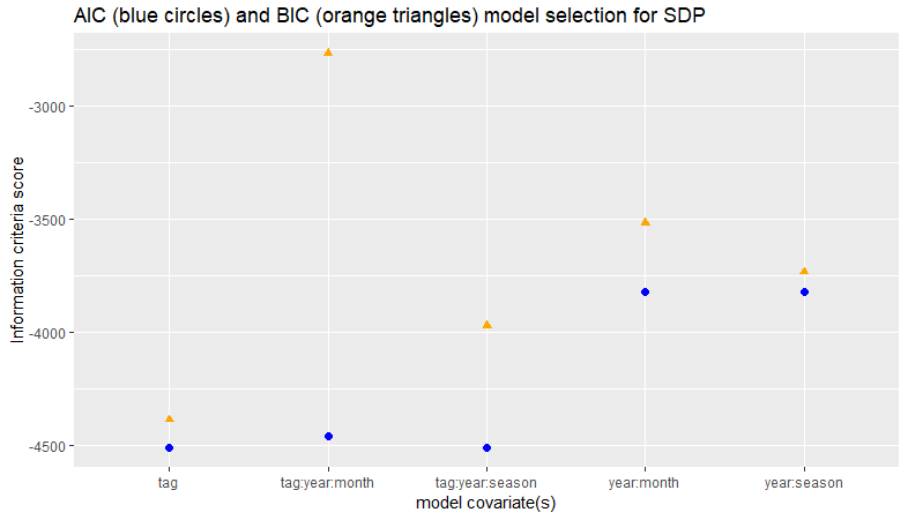

Figure III. 5 Performance of the models tested for straightness of a daily path (SDP) using the Akaike (AIC, shown in blue circles) and Bayesian information criteria (BIC, shown in orange triangles).

Best model assessment

See **Figure III. 3** above.

Model results

Table III. 9 Summary of the predictions generated by the best candidate model for straightness of a daily path (SPD), for each of birds analysed, with respective upper and lower confidence intervals (CI). Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	no. obs.	mean SDP	lower CI	upper CI	Deployment area
5215	59	0.797	0.773	0.821	Etosha NP
5403	346	0.701	0.686	0.717	Etosha NP
5404	537	0.629	0.610	0.645	Kunene Region
5784	255	0.528	0.500	0.556	Etosha NP
5785	405	0.596	0.571	0.621	Etosha NP
5786	413	0.643	0.626	0.661	Etosha NP
5787	322	0.624	0.599	0.647	Bwabwata NP
5788	226	0.679	0.648	0.708	Etosha NP
5789	143	0.664	0.636	0.690	Bwabwata NP
CAT1	316	0.599	0.573	0.626	Bwabwata NP
st2010-1330	424	0.747	0.730	0.765	Bwabwata NP
st2010-1332	929	0.777	0.764	0.790	Bwabwata NP
st2010-2607	560	0.803	0.787	0.818	Etosha NP
st2010-2608	436	0.761	0.731	0.787	Etosha NP
st2010-2609	320	0.734	0.708	0.758	Etosha NP
st2010-2697	445	0.741	0.720	0.759	Etosha NP
st2010-2700	465	0.710	0.692	0.729	Etosha NP

Table III. 10 Summary of the predictions generated by the second-best candidate model for straightness of a daily path (SPD), for each of birds analysed. The minima (min.) and maxima (max.) mean predictions with respective upper and lower confidence intervals (CI) shown for SPD. The respective time when those predictions were expected to occur are also shown: Yse – year-season, Se – season. Seasons: hot wet (1hw) - January to May, cold dry (2cd) - June to August, small rain (2sr) – September to December. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	no. seasons	min mean SDP	min lower CI	min upper CI	min Yse	min Se	max mean SDP	max lower CI	max upper CI	max Yse	max Se	Deployment area
5215	2	0.792	0.764	0.817	20173sr	3sr	0.802	0.753	0.844	20181hw	1hw	Etosha NP
5403	4	0.687	0.650	0.718	20171hw	1hw	0.714	0.668	0.763	20181hw	1hw	Etosha NP
5404	6	0.601	0.560	0.642	20173sr	3sr	0.698	0.624	0.772	20183sr	3sr	Kunene Region
5784	3	0.524	0.474	0.568	20173sr	3sr	0.547	0.491	0.599	20172cd	2cd	Etosha NP
5785	4	0.587	0.548	0.626	20181hw	1hw	0.662	0.604	0.716	20172cd	2cd	Etosha NP
5786	5	0.614	0.559	0.666	20172cd	2cd	0.885	0.786	0.945	20183sr	3sr	Etosha NP
5787	4	0.613	0.572	0.646	20181hw	1hw	0.650	0.605	0.695	20173sr	3sr	Bwabwata NP
5788	4	0.616	0.577	0.650	20173sr	3sr	0.755	0.651	0.840	20183sr	3sr	Etosha NP
5789	2	0.661	0.617	0.703	20181hw	1hw	0.669	0.636	0.701	20173sr	3sr	Bwabwata NP
CAT1	4	0.588	0.558	0.616	20181hw	1hw	0.691	0.570	0.794	20183sr	3sr	Bwabwata NP
st2010-1330	4	0.706	0.663	0.744	20151hw	1hw	0.771	0.741	0.799	20161hw	1hw	Bwabwata NP
st2010-1332	10	0.728	0.673	0.774	20181hw	1hw	0.807	0.781	0.831	20173sr	3sr	Bwabwata NP
st2010-2607	6	0.781	0.742	0.818	20182cd	2cd	0.868	0.754	0.942	20183sr	3sr	Etosha NP
st2010-2608	5	0.730	0.659	0.795	20173sr	3sr	0.866	0.730	0.944	20182cd	2cd	Etosha NP
st2010-2609	4	0.693	0.660	0.731	20172cd	2cd	0.802	0.797	0.807	20171hw	1hw	Etosha NP
st2010-2697	5	0.727	0.689	0.766	20172cd	2cd	0.761	0.717	0.802	20173sr	3sr	Etosha NP
st2010-2700	6	0.647	0.608	0.684	20172cd	2cd	0.780	0.717	0.837	20183sr	3sr	Etosha NP

Appendix IV Daily movement properties: combined properties

Table IV. 1 Contrasting the individual movement metrics for each of the birds that travelled the farthest and the least away from where they were first seen (the *travellers* and the *locals*, respectively). Results from the best predictive models are summarized: minima (min.) and maxima (max.) mean predictions with respective upper and lower confidence intervals (CI) shown for daily distance travelled (DDT, km), daily overall displacement (DOD, km), daily maximum displacement (DMD, km), straightness of a daily path (SPD). The respective time when those predictions were expected to occur are also shown: Ymo – year-month, Yse – year-season, Se – season. Seasons: hot wet (1hw) - January to May, cold dry (2cd) - June to August, small rain (2sr) – September to December.

	Tag ID	5784	5785	5788	5786	5789	st2010-2700
	Age	adult	immature	adult	adult	adult	sub-adult
	traveller / local	local	local	local	traveller	traveller	traveller
	Depl. Region	Kunene R	Etosha NP	Etosha NP	Etosha NP	Bwabwata NP	Etosha NP
	no. months	9	14	10	15	6	17
	no. seasons	6	3	4	4	2	6
DDT	min mean DDT	127.51	73.54	32.90	4.89680036	32.90	46.13
	min lower CI	95.41	53.49	32.28	0.472404887	32.28	32.59
	min upper CI	160.57	100.19	33.54	18.21044208	33.54	63.17
	min Ymo	201803	201806	201806	201809	201806	201807
	min Se	1hw	2cd	2cd	3sr	2cd	2cd
	max mean DDT	195.59	220.27	188.36	149.6235528	188.36	125.04
	max lower CI	152.07	167.30	150.05	130.6658033	150.05	103.55
	max upper CI	242.33	284.35	233.42	167.713699	233.42	146.27
	max Ymo	201711	201712	201711	201711	201711	201708
	max Se	3sr	3sr	3sr	3sr	3sr	2cd
DOD	mean DOD	34.63	46.08	46.84	45.89383285	47.16	42.81
	lower CI	28.56	41.91	40.41	39.24126852	34.28	37.01
	upper CI	41.97	50.37	53.72	54.60661851	62.92	49.93
DMD	min mean DMD	40.99	48.21	50.74	3.959	59.11	30.93
	min lower CI	33.99	42.01	40.91	0.391	48.14	19.75
	min upper CI	49.40	54.74	62.41	15.122	72.23	46.69
	min Yse	20181hw	20182cd	20181hw	20183sr	20181hw	20183sr
	min Se	1hw	2cd	1hw	3sr	1hw	3sr
	max mean DMD	59.75	70.77	67.35	65.684	61.59	63.50
	max lower CI	54.12	61.11	56.28	52.431	43.29	50.74
	max upper CI	65.57	81.37	78.68	81.741	86.76	78.18
	max Yse	20172cd	20172cd	20173sr	20173sr	20173sr	20173sr
	max Se	2cd	2cd	3sr	3sr	3sr	3sr
SDP- tag	mean SDP	0.528	0.596	0.679	0.643	0.664	0.710
	lower CI	0.500	0.571	0.648	0.626	0.636	0.692
	upper CI	0.556	0.621	0.708	0.661	0.690	0.729
SDP-season	min mean SDP	0.524	0.587	0.616	0.614	0.661	0.647
	min lower CI	0.474	0.548	0.577	0.559	0.617	0.608
	min upper CI	0.568	0.626	0.650	0.666	0.703	0.684
	min Yse	20173sr	20181hw	20173sr	20172cd	20181hw	20172cd
	min Se	3sr	1hw	3sr	2cd	1hw	2cd
	max mean SDP	0.547	0.662	0.755	0.885	0.669	0.780
	max lower CI	0.491	0.604	0.651	0.786	0.636	0.717
	max upper CI	0.599	0.716	0.840	0.945	0.701	0.837
	max Yse	20172cd	20172cd	20183sr	20183sr	20173sr	20183sr
	max Se	2cd	2cd	3sr	3sr	3sr	3sr

Table IV. 2 Inspection of nine trips made by the bird that recorded the largest daily distance travelled (DDT; a *local*, 5785) and the three birds that travelled the farthest away from where they were first seen (the *travellers*: 5786, 5789, and st2010-2700). A trip reference is shown to match the map below (**Figure IV. 1**), as well as the respective number of days, start and end date. The date to the farthest location in each trip is also shown to illustrate the maximum displacement from the start of the trip; the number of days it took to reach that farthest location is shown as well as the total distance flown (km).

Tag ID	Trip ref.	no. days	Start date	End date	Date farthest	no. days to farthest	Distance (km)
5785	1.1	1	2017-11-13	2017-11-13	2017-11-13	1	416.10
5786	2.1	8	2017-07-20	2017-07-27	2017-07-27	8	622.39
5786	2.2	6	2017-07-30	2017-08-04	2017-08-01	3	46.79
5786	2.3	10	2017-09-20	2017-09-29	2017-09-29	10	654.74
5786	2.4	8	2017-11-12	2017-11-19	2017-11-19	8	422.89
5789	3.1	15	2017-10-31	2017-11-14	2017-11-13	14	1,110.78
5789	3.2	15	2018-03-01	2018-0315	2018-03-15	15	923.59
st2010-2700	4.1	29	2017-10-27	2017-11-24	2017-11-21	26	1,404.15
st2010-2700	4.2	25	2017-12-24	2018-01-17	2018-01-17	25	971.73

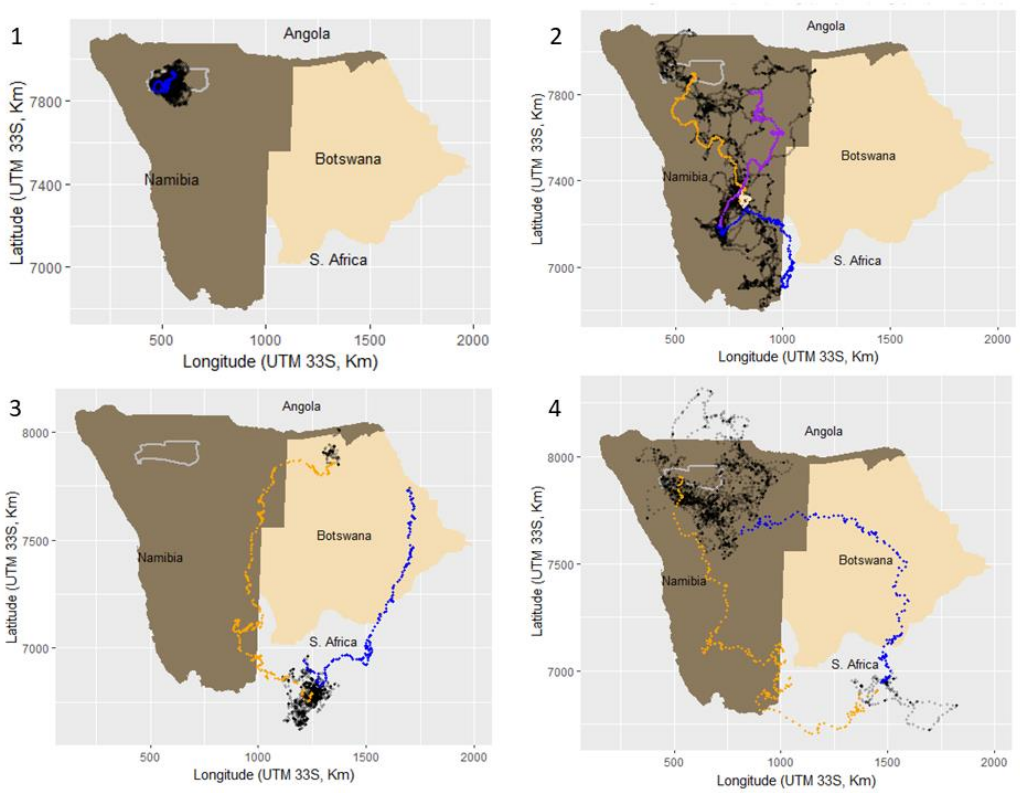

Figure IV. 1 Visual inspection of the trips described above (**Table IV. 2**) coloured against all the locations for each bird.1- 5785 on the day of maximum daily distance travelled (blue); 2- 5786 on four trips as described above (2.1 in orange, 2.2 in beige, 2.3 in purple, 2.4 in blue); 3- 5789 on two trips (3.1 in orange, 3.2 in blue); and 4- st2010-2700 (4.1 in orange, 4.2 in blue).

Appendix V Range areas: sizes and temporal variation for each vulture

Table V. 1 Summary of the size of each estimated range area per individual. The number of months per bird is shown. The mean size of range areas (home range (HR), and core area (CA), sq.km) are shown with 95% confidence limits (CI) (inside square brackets) and range values (round brackets). The ratio of core area to home range (CA/HR), is also shown with 95%CI and range values. Immature and sub-adult vultures are highlighted in bold.

Species and tag ID	Number of months	HR (sq.km)	CA (sq.km)	CA/ HR
White-backed vultures				
5403	11	29,683.47 [10,644.06;84,512.11] (9,544.5-93,723.38)	8,604.61 [2,837.98;24,353.06] (2,502.93-27,884.97)	0.30 [0.24;0.47] (0.24-0.52)
5404	20	19,794.44 [2,067.32;70,007.74] (1,617.78-82,289.38)	5,164.93 [539.35;18,942.56] (408.2-21,964.15)	0.26 [0.19;0.29] (0.18-0.29)
5784	8	10,635.51 [5,623.53;17,102.26] (5,340.98-17,405.08)	2,101.84 [1,171.44;3,061.59] (1,106.97-3,098.62)	0.21 [0.16;0.28] (0.16-0.28)
5785	15	9,643.29 [4,765.61;16,900.6] (4,462.8-17,436.62)	2,352.28 [1,063.91;3,843.82] (1,034.12-3,884.62)	0.24 [0.20;0.32] (0.20-0.33)
5786	14	51,452.86 [2,495.46;110,065.8] (1,174.62-110,664.5)	14,496.82 [600.9;33,249.35] (346.95-36,029.53)	0.28 [0.22;0.32] (0.22-0.33)
5787	13	37,543.46 [2,102.28;104,599.5] (2,091.18-108,351.2)	9,253.57 [453.48;29,501.66] (436.32-31,544.12)	0.24 [0.17;0.30] (0.15-0.31)
5788	11	20,059.89 [5,867.83;50,554.01] (4,036.4-56,858.57)	5,625.11 [1,653.65;14,750.69] (1,251.2-16,376)	0.29 [0.22;0.40] (0.22-0.42)
5789	5	44,359.64 [14,823.55;99,819.09] (14,221.55-106,102.4)	10,649.43 [2,864.08;21,806.86] (2,733.95-22,752.8)	0.24 [0.19;0.34] (0.19-0.35)
st2010-1332	35	12,513.89 [2,135.05;39,693.36] (1,278.83-67,788.9)	3,051.45 [421.82;9,832.29] (251.95-21,035.08)	0.23 [0.17;0.31] (0.15-0.33)
st2010-2607	21	25,385.94 [7,480.33;46,300.99] (7,469.35-50,255.82)	6,187.69 [2,058.53;12,541.96] (1,915.38-14,703.4)	0.25 [0.18;0.31] (0.17-0.32)
st2010-2608	17	10,651.98 [3,560.43;34,249.88] (3,132.97-39,245.75)	2,463.38 [846.68;6,747.57] (775.88-7,154.3)	0.24 [0.17;0.32] (0.16-0.34)
st2010-2609	11	29,816.74 [9,341.36;86,700.01] (9,316.98-96,499.25)	7,381.75 [2,012.44;24,029.54] (1,907.22-26,951.4)	0.23 [0.15;0.31] (0.15-0.32)
st2010-2697	15	4,759.23 [2,936.82;6,614.39] (2,745.5-6,767.07)	1,107.5 [562.43;1,639.55] (514.19-1,737.8)	0.24 [0.13;0.33] (0.12-0.34)
st2010-2700	18	63,403.75 [11,195.47;141,645.9] (7,757.55-145,449.8)	18,081.88 [3,118.15;44,380.61] (1,726.6-48,528.6)	0.29 [0.23;0.33] (0.22-0.33)
Hooded vultures				
CAT1	13	2,127.75 [652.59;4,429.93] (607.2-4,455.9)	493.05 [146.89;1,011.17] (141.5-1,046.67)	0.24 [0.16;0.30] (0.15-0.31)
st2010-1330	13	1,602.48 [429.15;3,738.87] (369.65-3,823.6)	403.19 [57.83;1,616.67] (49.05-2,006.53)	0.21 [0.13;0.45] (0.13-0.52)

Table V. 2 Summary of the estimated monthly home range areas (HR), for each of birds analysed. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	n.months	min mean HR	min lower CI	min upper CI	min Ymo	min Yse	max mean HR	max lower CI	max upper CI	max Ymo	max Yse	Deployment area
5403	11	9,544.50	8,125.00	11,150.63	201705	20171hw	93,723.38	83,999.38	103,300.00	201706	20172cd	Etosha NP
5404	20	1,617.78	1,375.00	1,925.00	201803	20181hw	82,289.38	69,517.50	103,956.25	201705	20171hw	Kunene Region
5784	8	5,340.98	4,224.38	7,276.88	201803	20181hw	17,405.08	15,825.00	18,675.00	201712	20173sr	Etosha NP
5785	15	4,462.80	4,000.00	5,000.00	201809	20183sr	17,436.63	14,825.00	20,500.63	201804	20181hw	Etosha NP
5786	14	1,174.63	375.00	2,300.63	201808	20182cd	110,664.50	95,673.75	130,206.25	201710	20173sr	Etosha NP
5787	13	2,091.18	1,675.00	2,800.63	201803	20181hw	108,351.23	87,125.00	137,931.25	201809	20183sr	Bwabwata NP
5788	11	4,036.40	2,850.00	5,879.38	201804	20181hw	56,858.58	46,098.75	64,850.63	201808	20182cd	Etosha NP
5789	5	14,221.55	11,499.38	17,425.00	201712	20173sr	106,102.43	84,115.00	126,177.50	201711	20173sr	Bwabwata NP
CAT1	13	607.20	350.00	875.00	201807	20182cd	4,455.90	3,625.00	5,350.00	201803	20181hw	Bwabwata NP
st2010-1330	13	369.65	250.00	525.00	201504	20151hw	3,823.60	875.00	5,225.00	201509	20153sr	Bwabwata NP
st2010-1332	35	1,278.83	950.00	1,775.00	201609	20163sr	67,788.90	56,920.00	81,401.25	201510	20153sr	Bwabwata NP
st2010-2607	21	7,469.35	6,400.00	8,800.63	201707	20172cd	50,255.83	44,173.13	60,281.25	201705	20171hw	Etosha NP
st2010-2608	17	3,132.98	2,425.00	4,325.63	201804	20181hw	39,245.75	29,998.75	47,755.00	201712	20173sr	Etosha NP
st2010-2609	11	9,316.98	6,949.38	11,676.25	201803	20181hw	96,499.25	76,424.38	119,028.13	201710	20173sr	Etosha NP
st2010-2697	15	2,745.50	2,476.98	3,001.10	201803	20181hw	6,767.07	5,573.90	7,632.20	201706	20172cd	Etosha NP
st2010-2700	18	7,757.55	5,849.38	10,100.00	201805	20181hw	145,449.78	128,721.88	168,012.50	201710	20173sr	Etosha NP

Table V. 3 Summary of the estimated monthly core areas (CA), for each of birds analysed. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	n.months	min mean CA	min lower CI	min upper CI	min Ymo	min Yse	max mean CA	max lower CI	max upper CI	max Ymo	max Yse	Deployment area
5403	11	2,502.93	2,000.00	3,150.00	201705	20171hw	27,884.98	22,799.38	33,575.63	201706	20172cd	Etosha NP
5404	20	408.20	325.00	525.00	201803	20181hw	21,964.15	16,047.50	30,500.63	201705	20171hw	Kunene Region
5784	8	1,106.98	850.00	1,525.63	201803	20181hw	3,098.63	2,625.00	3,725.00	201708	20172cd	Etosha NP
5785	15	1,034.13	825.00	1,275.00	201809	20183sr	3,884.63	2,824.38	5,350.00	201804	20181hw	Etosha NP
5786	14	346.95	50.00	1,050.00	201808	20182cd	36,029.53	28,573.13	44,555.63	201710	20173sr	Etosha NP
5787	13	436.33	350.00	575.00	201803	20181hw	31,544.13	25,074.38	41,061.25	201809	20183sr	Bwabwata NP
5788	11	1,251.20	950.00	1,925.00	201804	20181hw	16,376.00	11,950.00	22,701.25	201808	20182cd	Etosha NP
5789	5	2,733.95	2,225.00	3,650.00	201712	20173sr	22,752.80	14,948.75	35,476.88	201711	20173sr	Bwabwata NP
CAT1	13	141.50	50.00	300.00	201807	20182cd	1,046.68	875.00	1,250.63	201803	20181hw	Bwabwata NP
st2010-1330	13	49.05	25.00	75.00	201504	20151hw	2,006.53	449.38	2,750.00	201509	20153sr	Bwabwata NP
st2010-1332	35	251.95	150.00	400.00	201609	20163sr	21,035.08	15,623.75	27,278.13	201510	20153sr	Bwabwata NP
st2010-2607	21	1,915.38	1,450.00	2,450.63	201707	20172cd	14,703.40	9,625.00	20,400.63	201705	20171hw	Etosha NP
st2010-2608	17	775.88	600.00	1,125.00	201705	20171hw	7,154.30	5,499.38	9,675.00	201707	20172cd	Etosha NP
st2010-2609	11	1,907.23	1,399.38	2,800.63	201803	20181hw	26,951.40	17,900.00	39,401.25	201710	20173sr	Etosha NP
st2010-2697	15	514.19	397.98	674.03	201803	20181hw	1,737.80	1,312.00	2,347.15	201802	20181hw	Etosha NP
st2010-2700	18	1,726.60	1,274.38	2,425.00	201805	20181hw	48,528.60	36,897.50	61,180.00	201710	20173sr	Etosha NP

Table V. 4 Summary of the estimated monthly ratio between home range and core areas (ra, CA/HR), for each of birds analysed. Tag ID for white-backed vultures shown in black, sub-adult and immature highlighted in bold; hooded vultures highlighted in blue.

Tag ID	n.months	min mean ratio	min lower CI	min upper CI	min Ymo	min Yse	max mean ratio	max lower CI	max upper CI	max Ymo	max Yse	Deployment area
5403	11	0.242	0.199	0.303	201710	20173sr	0.522	0.200	1.000	201803	20181hw	Etosha NP
5404	20	0.185	0.166	0.224	201810	20183sr	0.294	0.260	0.321	201802	20181hw	Kunene Region
5784	8	0.158	0.114	0.239	201712	20173sr	0.282	0.266	0.297	201709	20173sr	Etosha NP
5785	15	0.202	0.166	0.251	201805	20181hw	0.328	0.303	0.351	201802	20181hw	Etosha NP
5786	14	0.215	0.193	0.245	201809	20183sr	0.326	0.279	0.368	201710	20173sr	Etosha NP
5787	13	0.154	0.094	0.267	201711	20173sr	0.310	0.288	0.327	201712	20173sr	Bwabwata NP
5788	11	0.216	0.192	0.245	201810	20183sr	0.424	0.096	0.523	201809	20183sr	Etosha NP
5789	5	0.192	0.166	0.238	201712	20173sr	0.350	0.326	0.382	201803	20181hw	Bwabwata NP
CAT1	13	0.148	0.115	0.204	201712	20173sr	0.308	0.274	0.341	201802	20181hw	Bwabwata NP
st2010-1330	13	0.131	0.087	0.188	201507	20152cd	0.525	0.517	1.000	201509	20153sr	Bwabwata NP
st2010-1332	35	0.154	0.127	0.210	201505	20151hw	0.334	0.288	0.376	201701	20171hw	Bwabwata NP
st2010-2607	21	0.174	0.126	0.229	201805	20181hw	0.324	0.297	0.350	201807	20182cd	Etosha NP
st2010-2608	17	0.156	0.101	0.237	201712	20173sr	0.335	0.259	0.417	201811	20183sr	Etosha NP
st2010-2609	11	0.150	0.111	0.215	201801	20181hw	0.317	0.267	0.351	201709	20173sr	Etosha NP
st2010-2697	15	0.121	0.075	0.213	201804	20181hw	0.339	0.320	0.357	201801	20181hw	Etosha NP
st2010-2700	18	0.223	0.198	0.262	201805	20181hw	0.334	0.299	0.365	201807	20182cd	Etosha NP

Appendix VI Range areas: spatial extent for each vulture

Home range

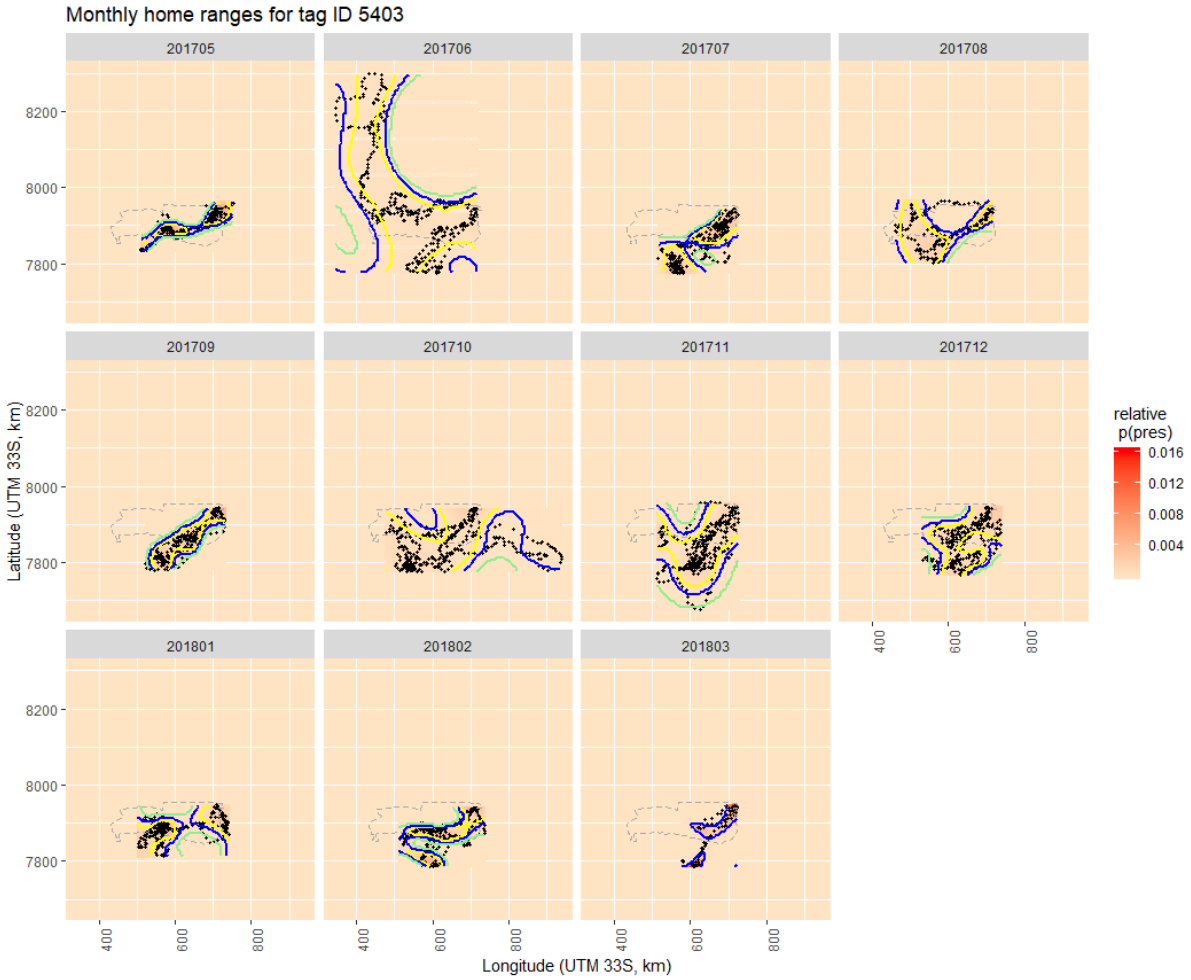

Figure VI. 1 Variation in the mean monthly home range in terms of geographic location, for bird ID 5403. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

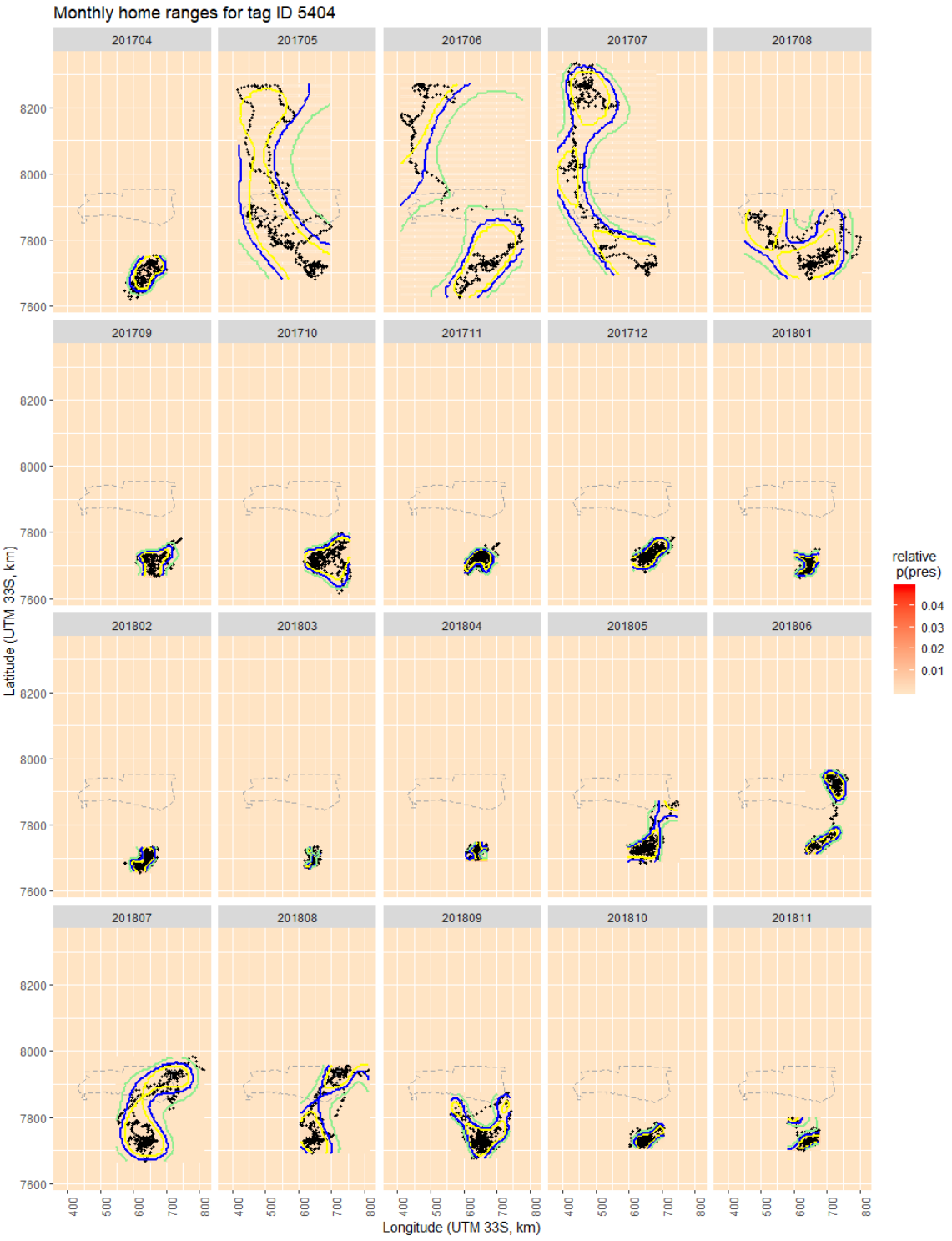

Figure VI. 2 Variation in the mean monthly home range in terms of geographic location, for bird ID 5404. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

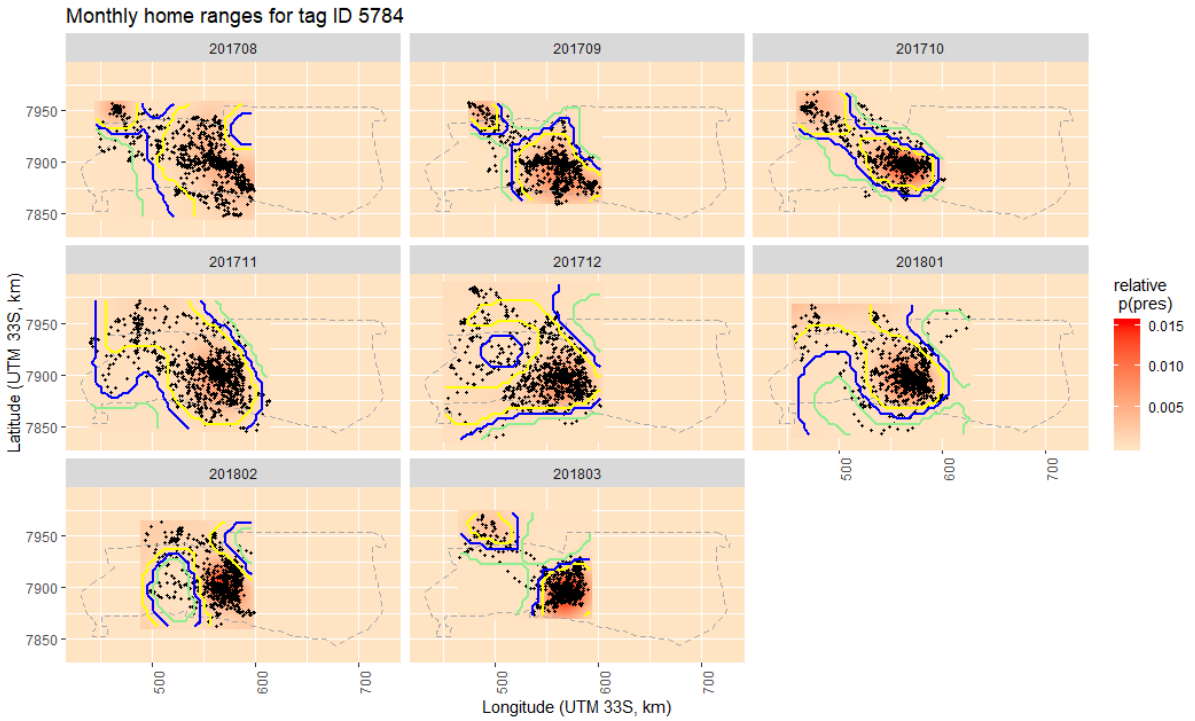

Figure VI. 3 Variation in the mean monthly home range in terms of geographic location, for bird ID 5784. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

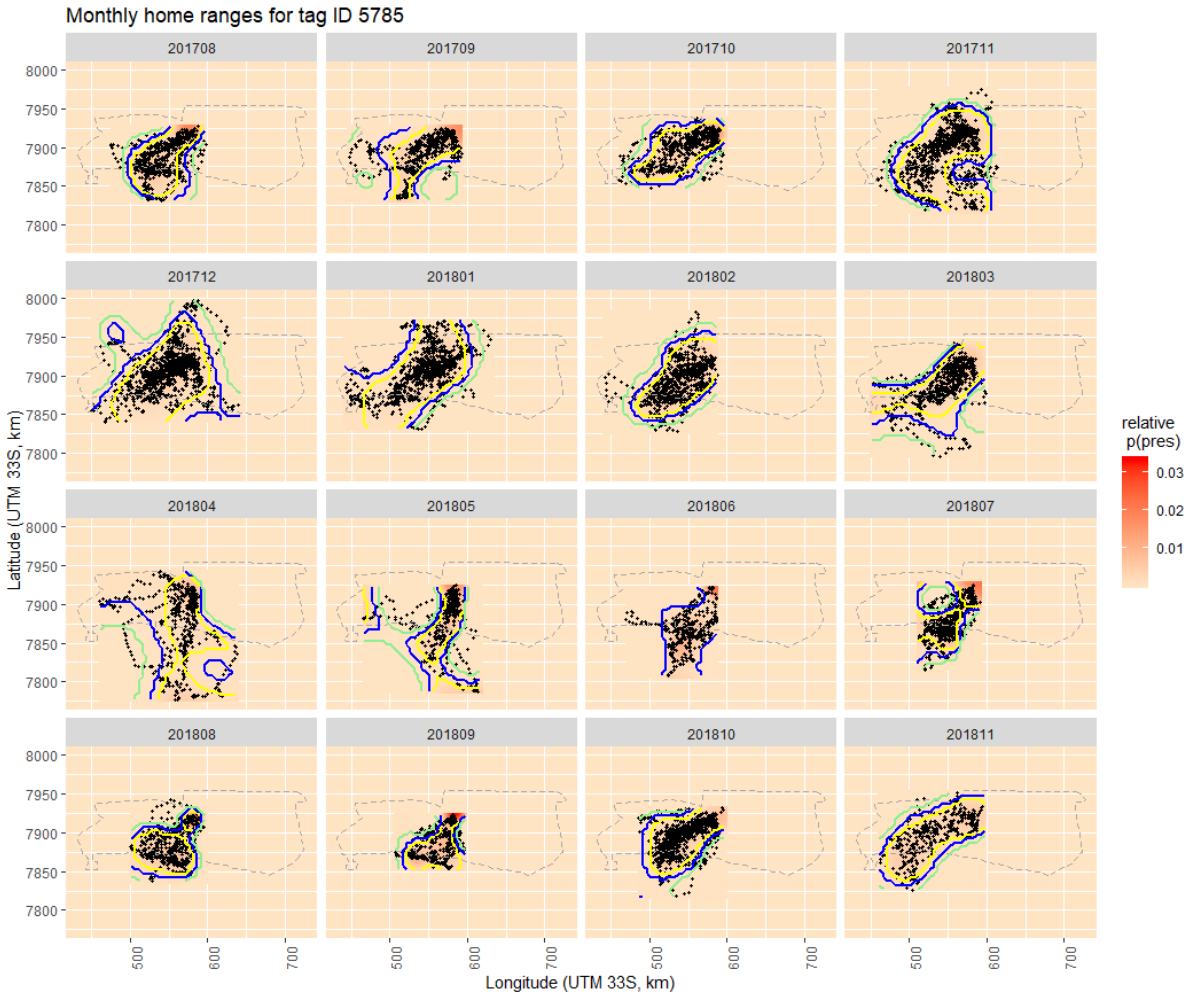

Figure VI. 4 Variation in the mean monthly home range in terms of geographic location, for bird ID 5785. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

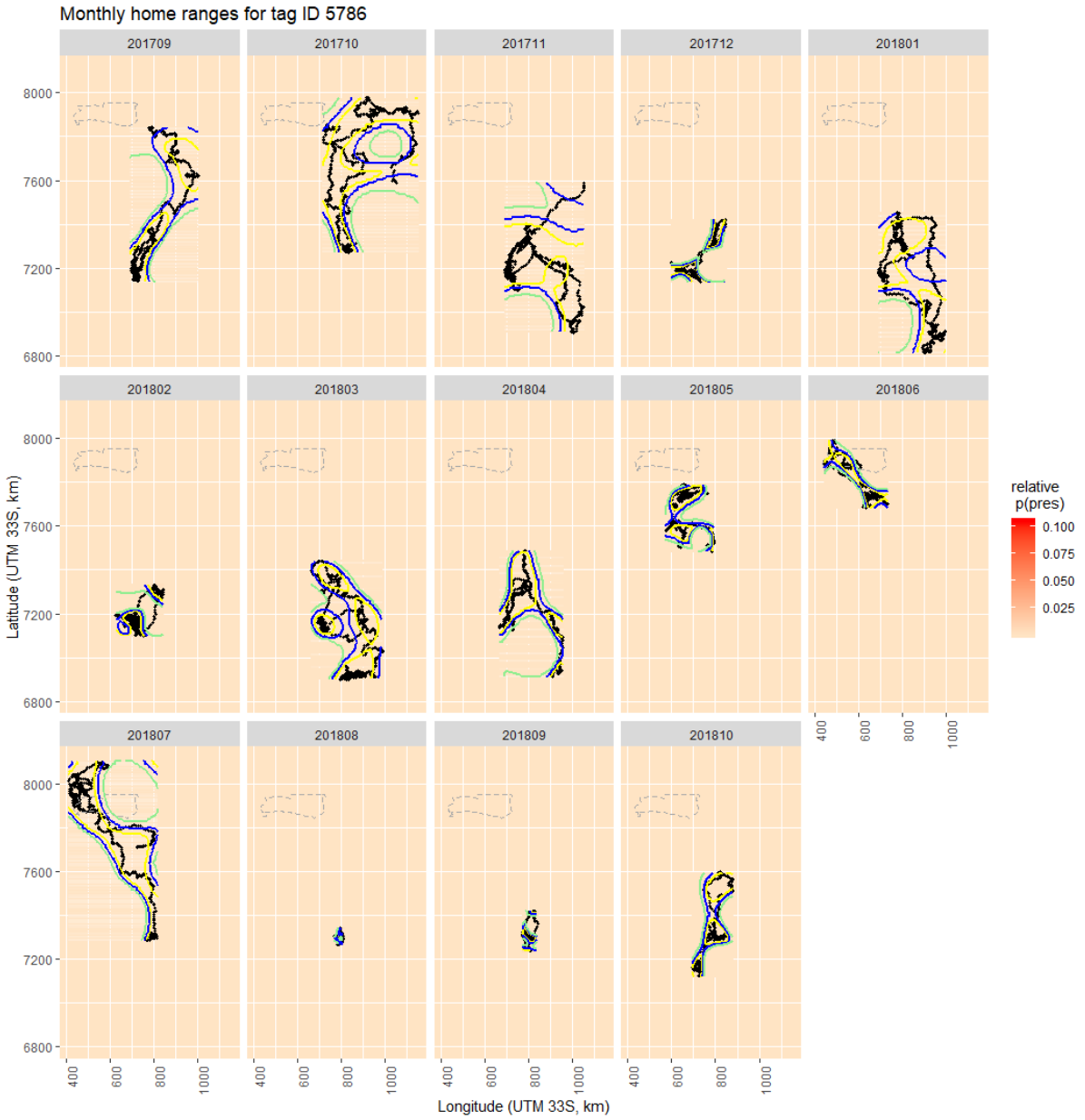

Figure VI. 5 Variation in the mean monthly home range in terms of geographic location, for bird ID 5786. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

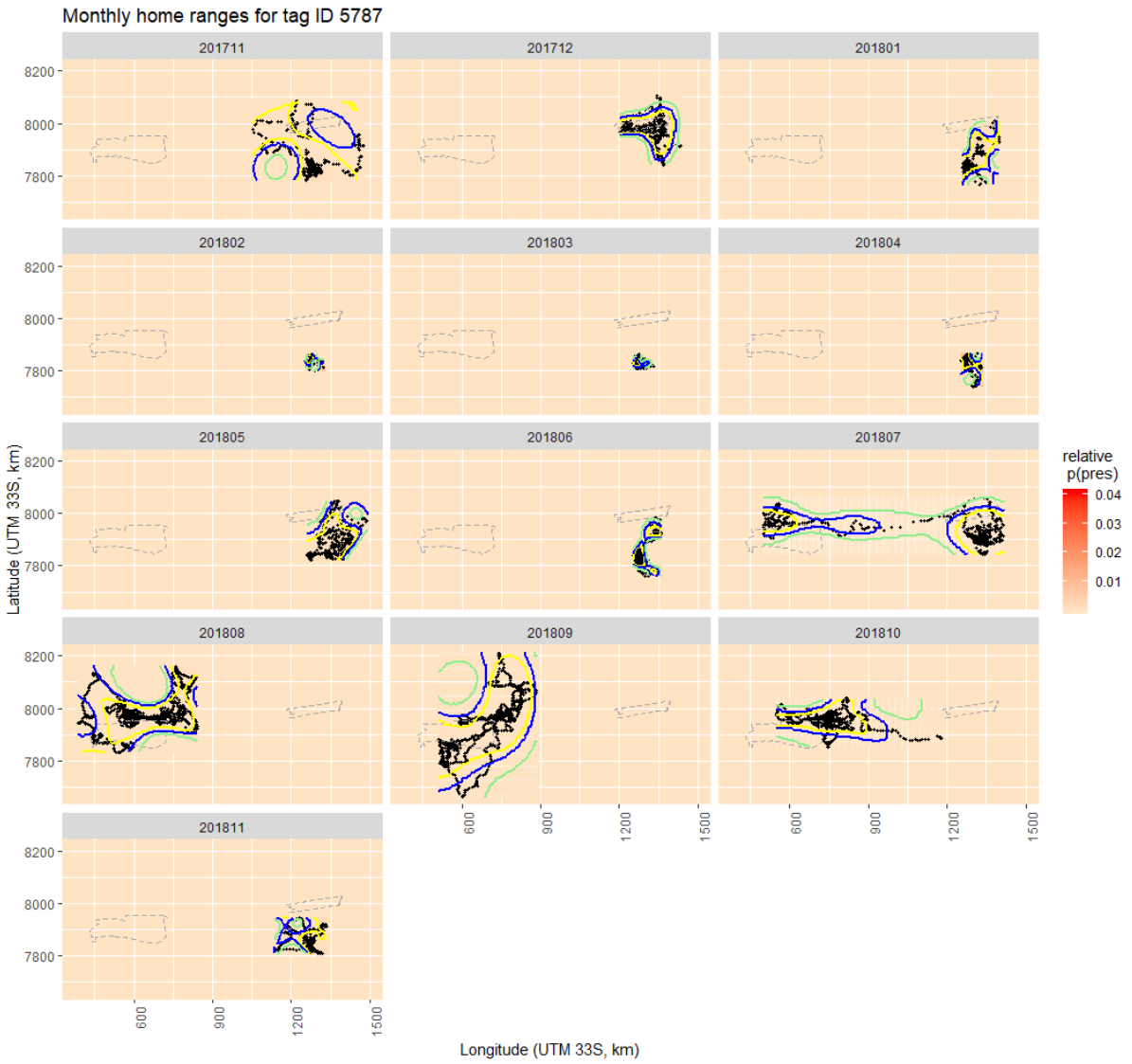

Figure VI. 6 Variation in the mean monthly home range in terms of geographic location, for bird ID 5787. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha and Bwabwata (on the NE) National Parks (dashed grey line) are shown for reference.

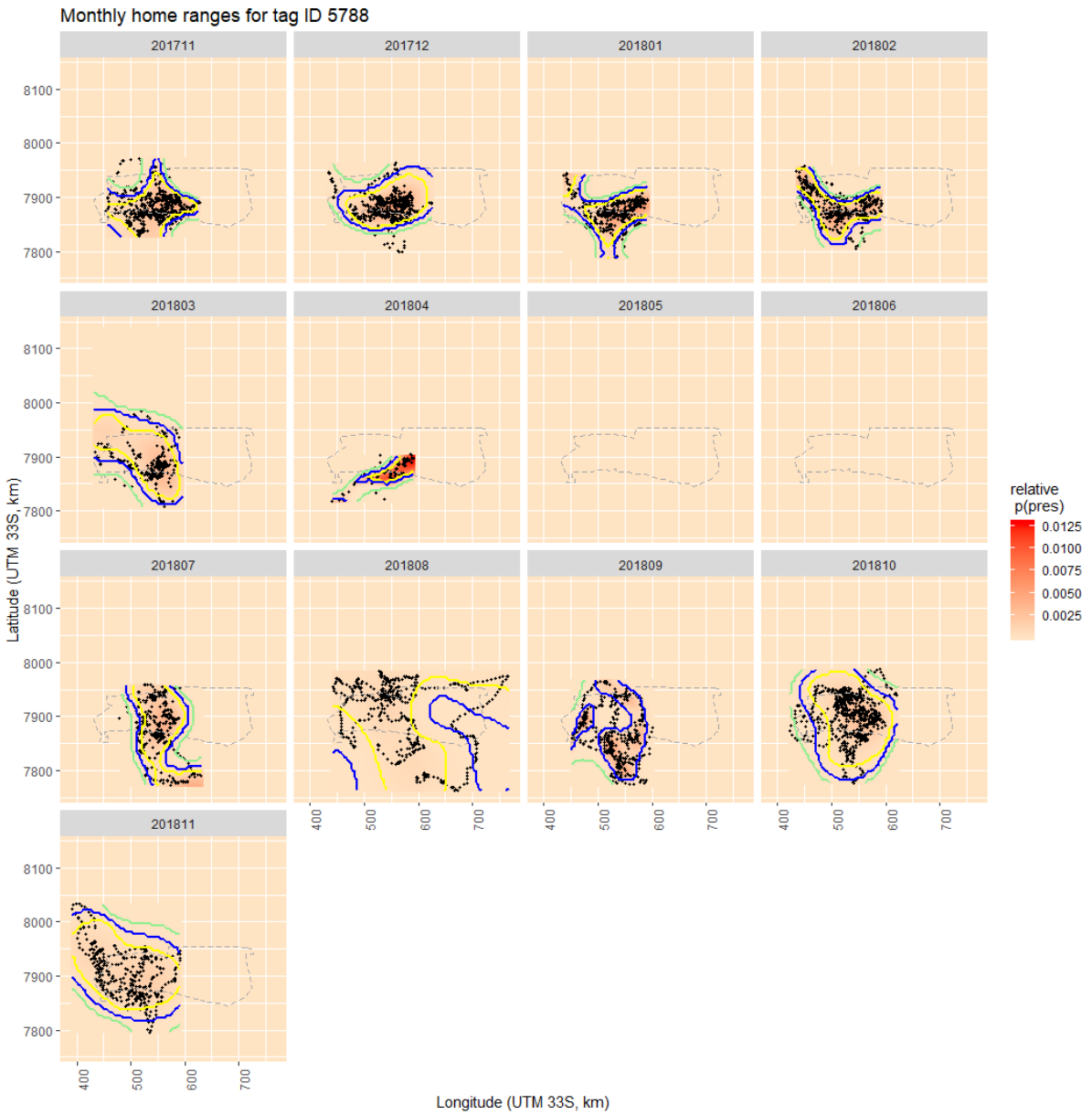

Figure VI. 7 Variation in the mean monthly home range in terms of geographic location, for bird ID 5788. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

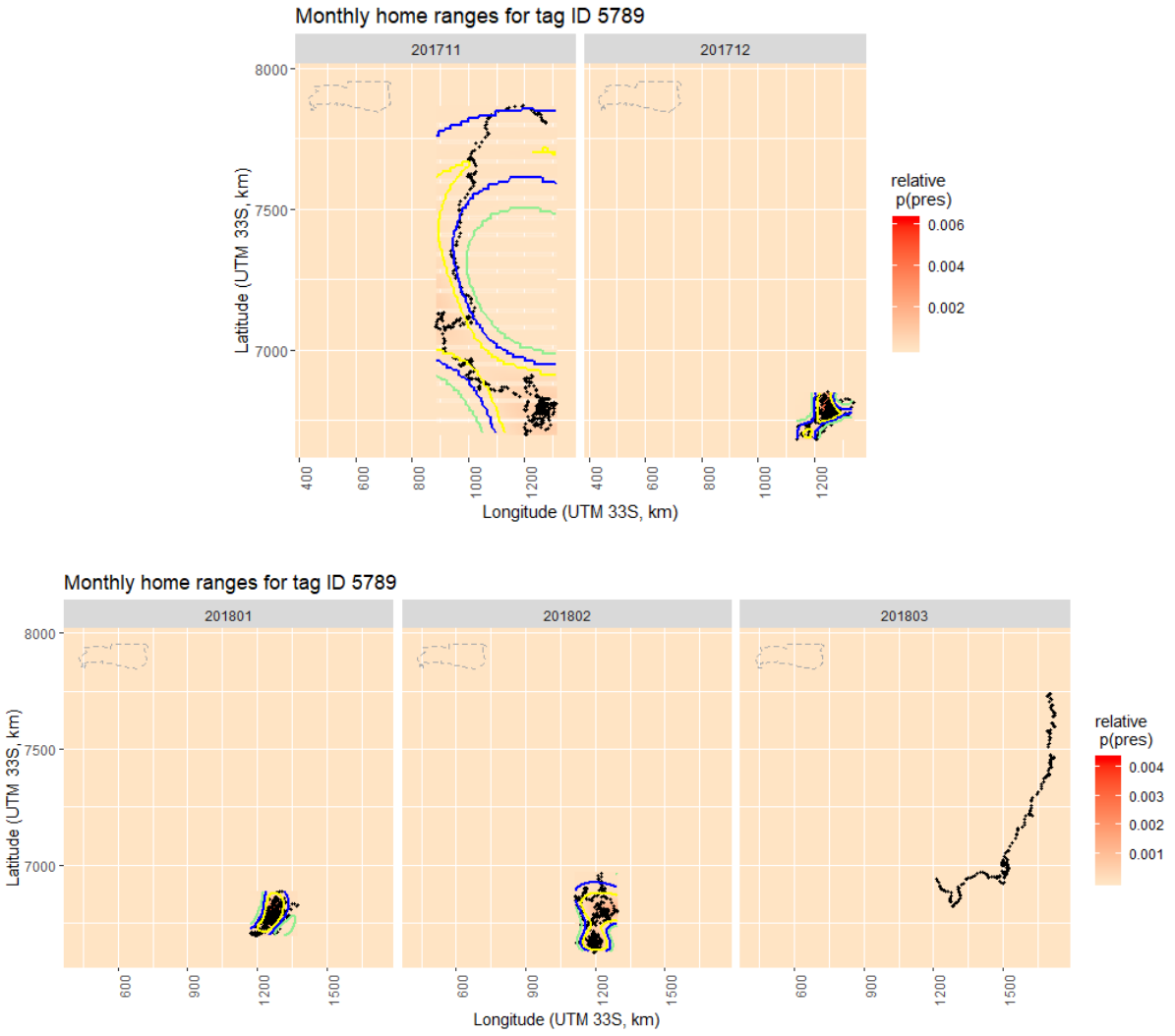

Figure VI. 8 Variation in the mean monthly home range in terms of geographic location, for bird ID 5789. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference. The plotting engine in use failed displaying the contours and parts of the probability raster for the last map.

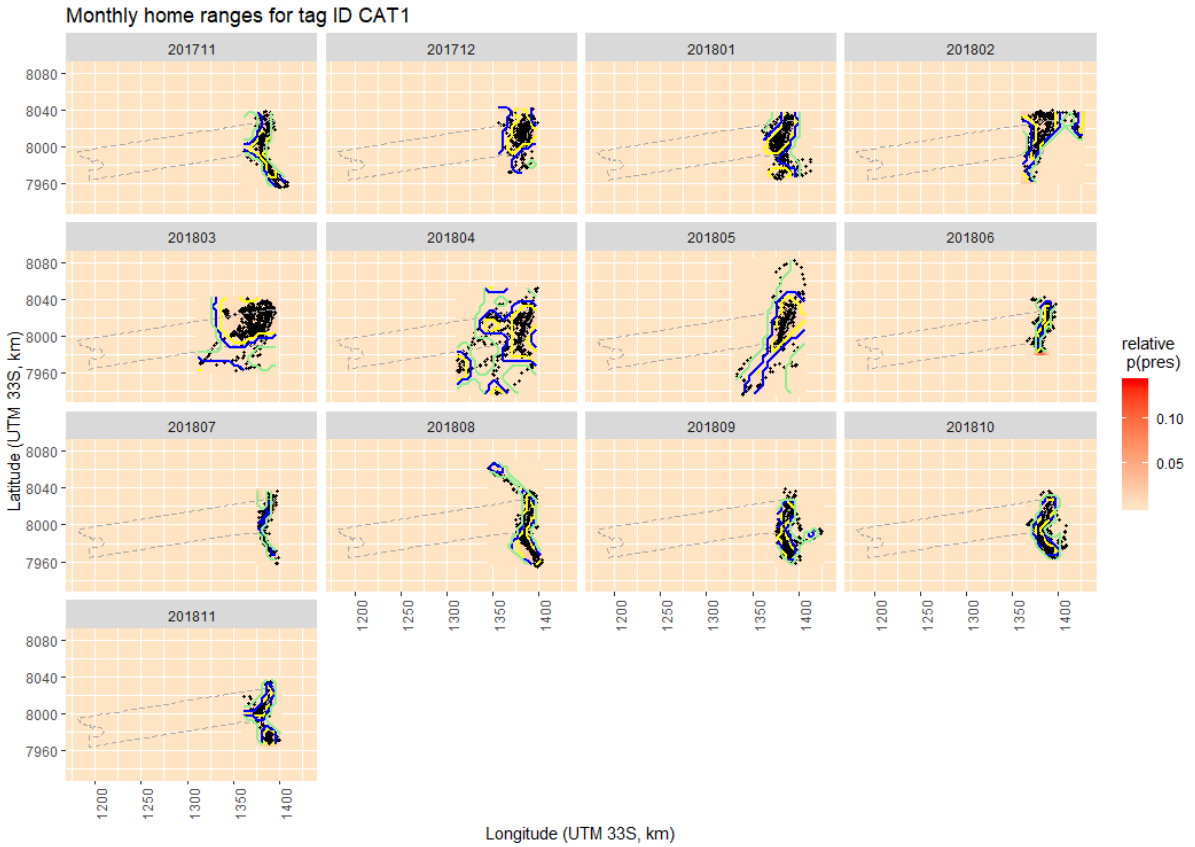

Figure VI. 9 Variation in the mean monthly home range in terms of geographic location, for bird ID CAT1. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Park (dashed grey line) shown for reference.

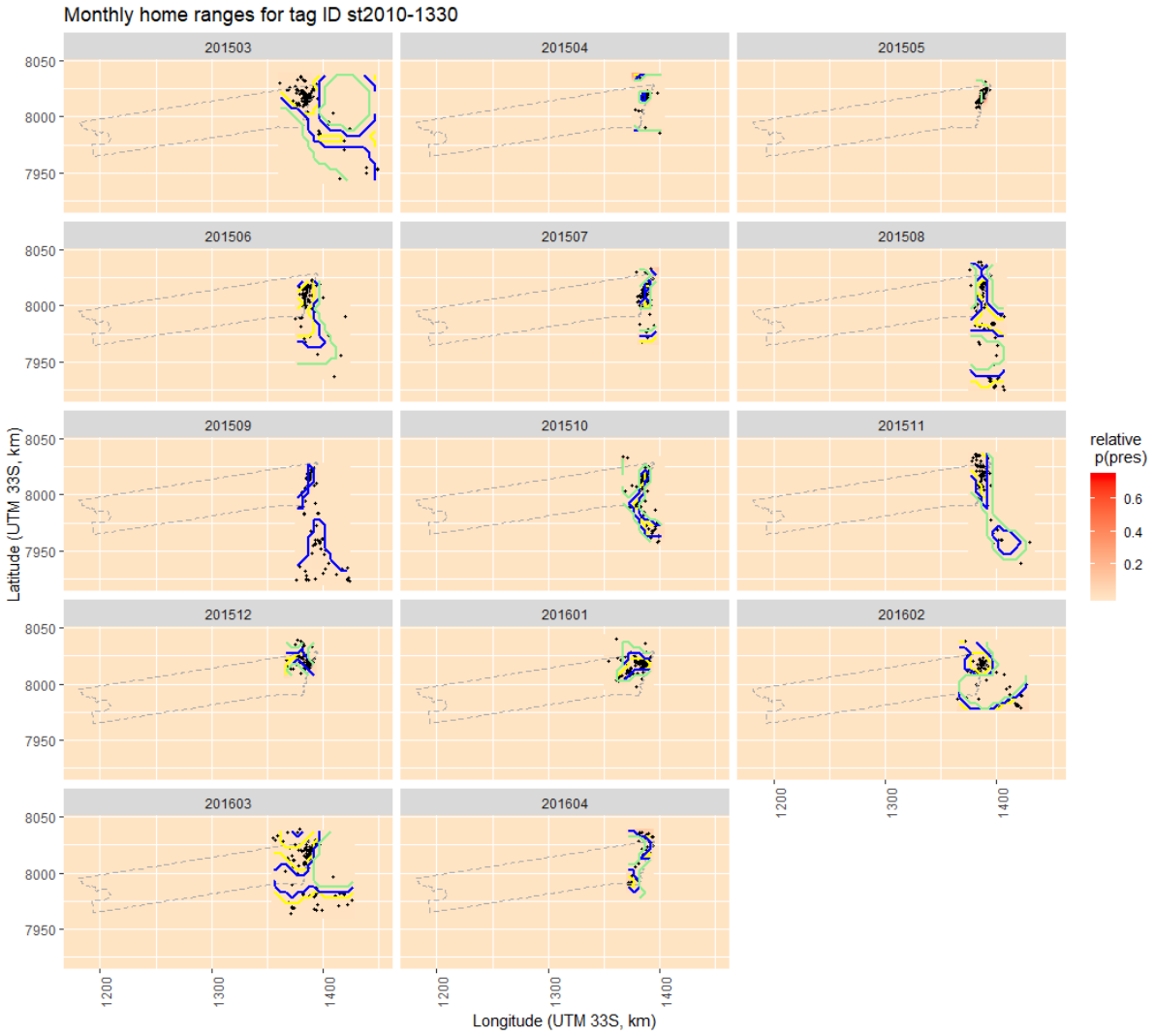

Figure VI. 10 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-1330. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Park (dashed grey line) shown for reference.

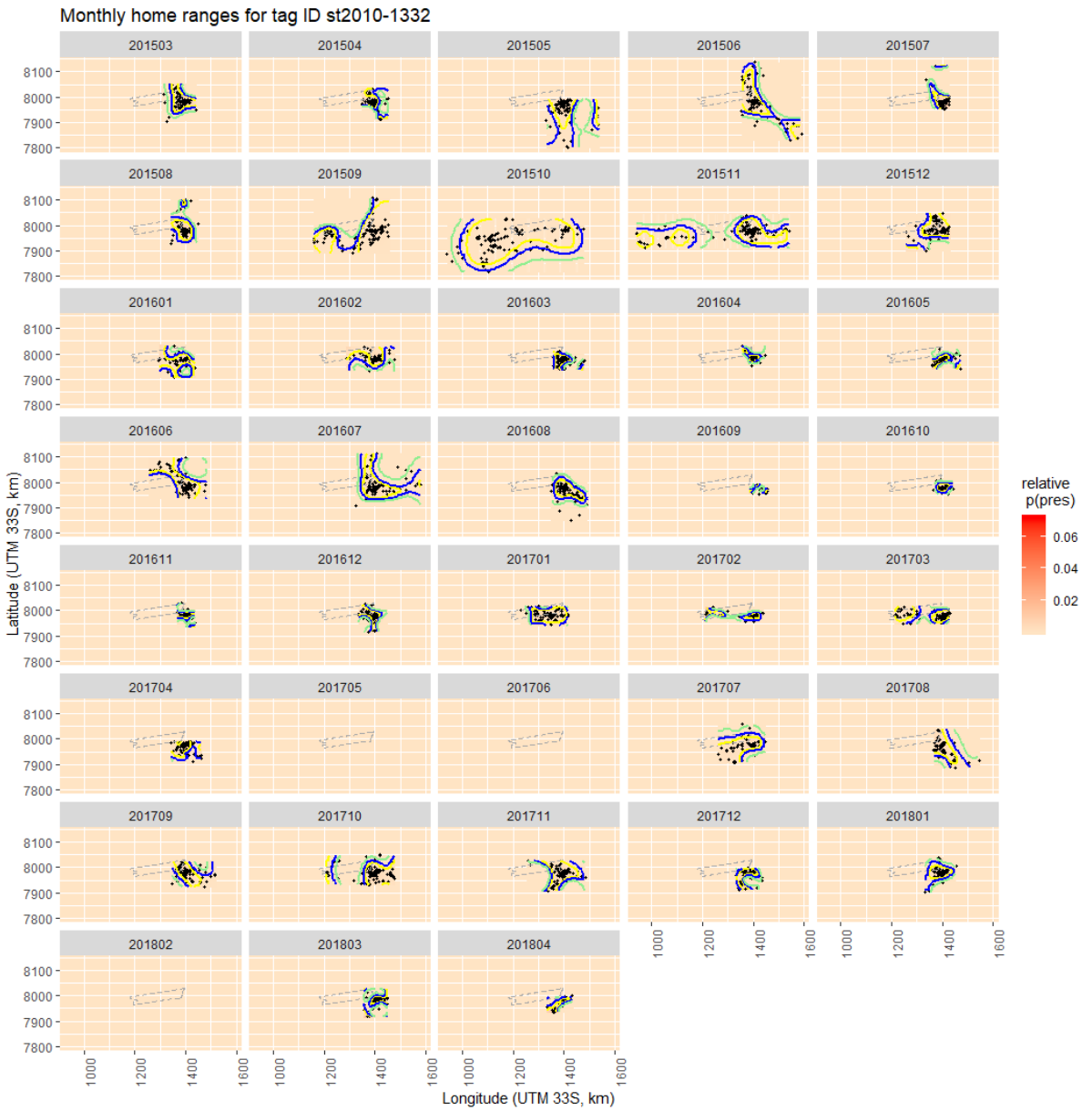

Figure VI. 11 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-1332. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Park (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

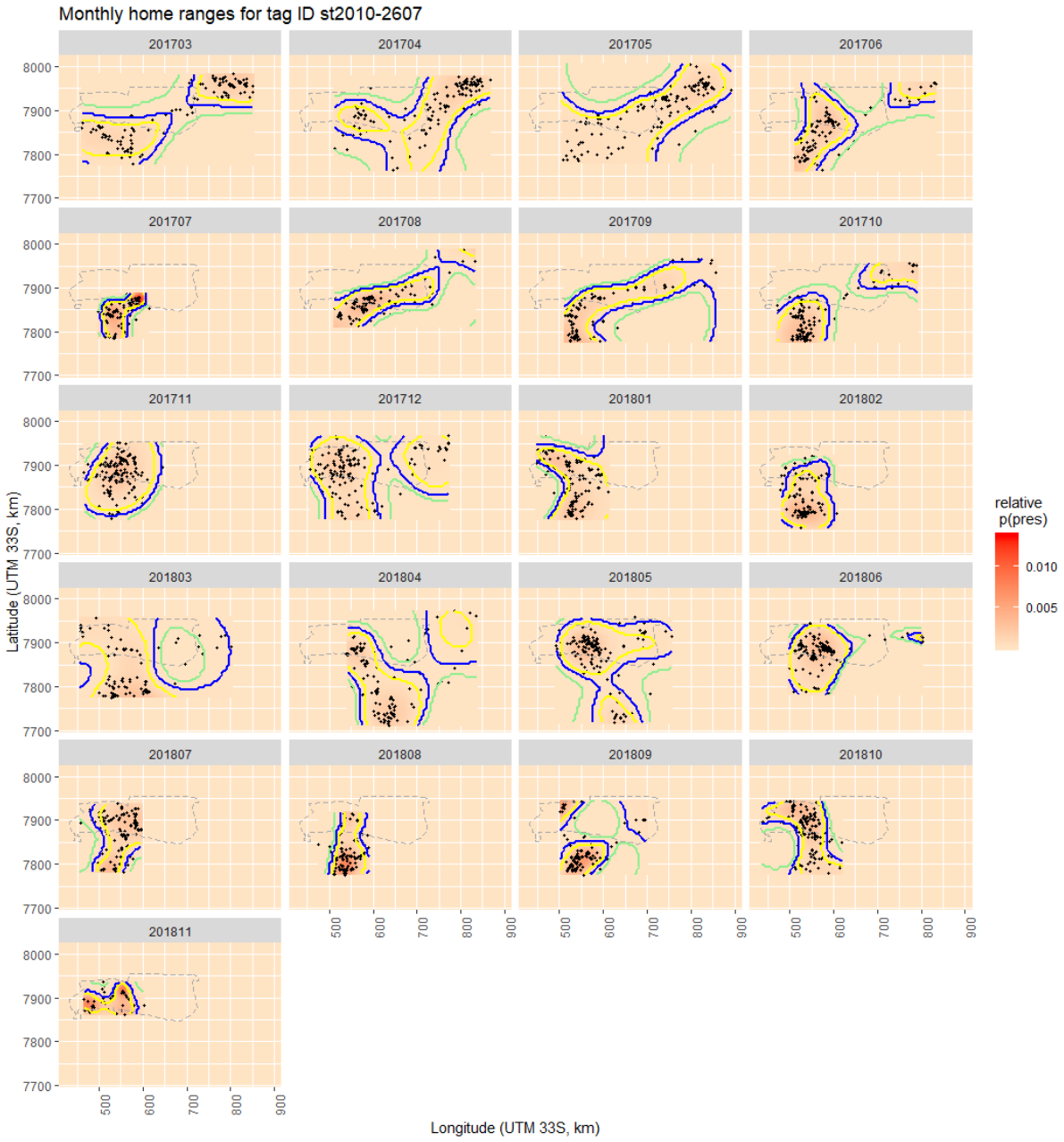

Figure VI. 12 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-2607. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

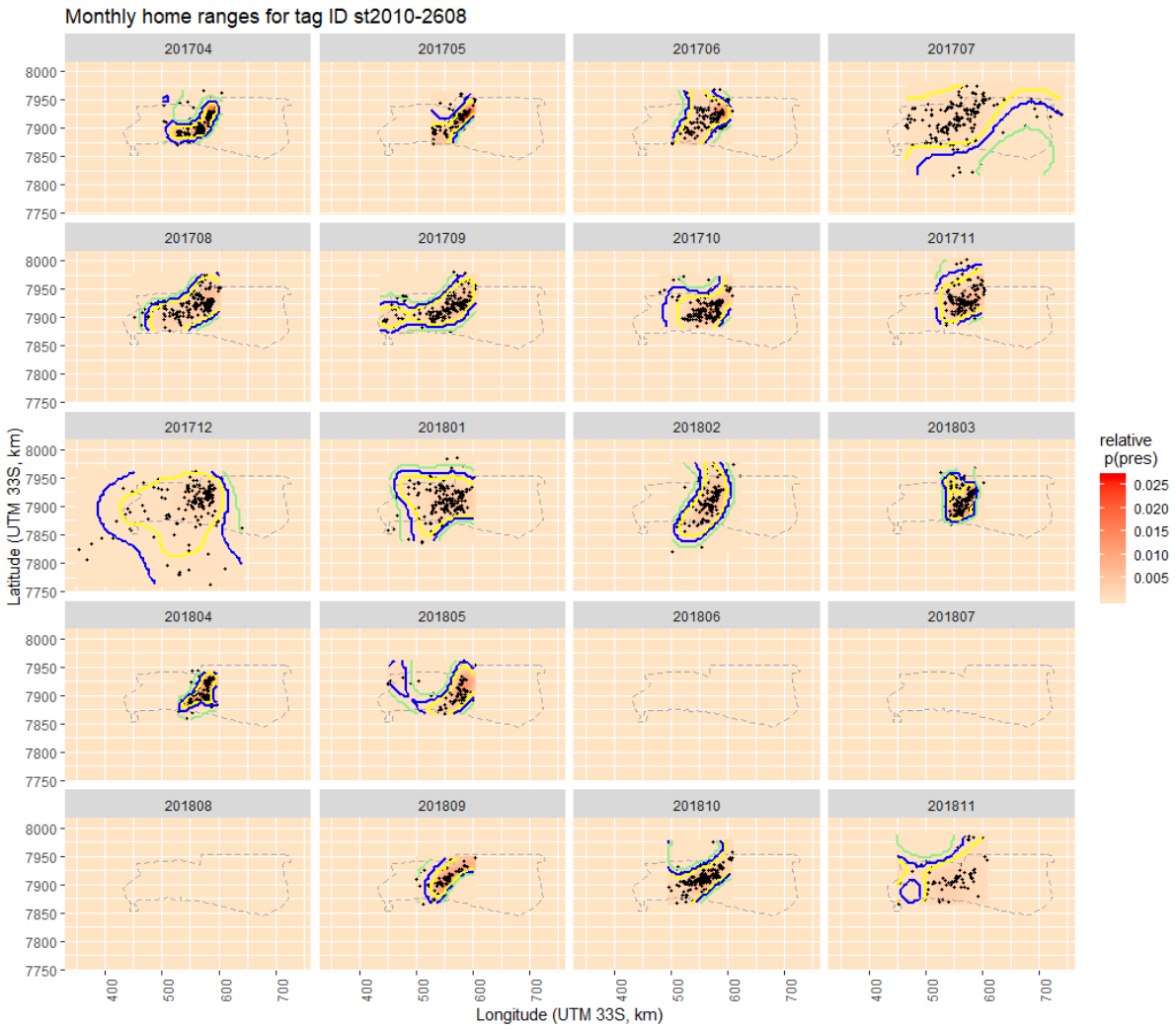

Figure VI. 13 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-2608. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

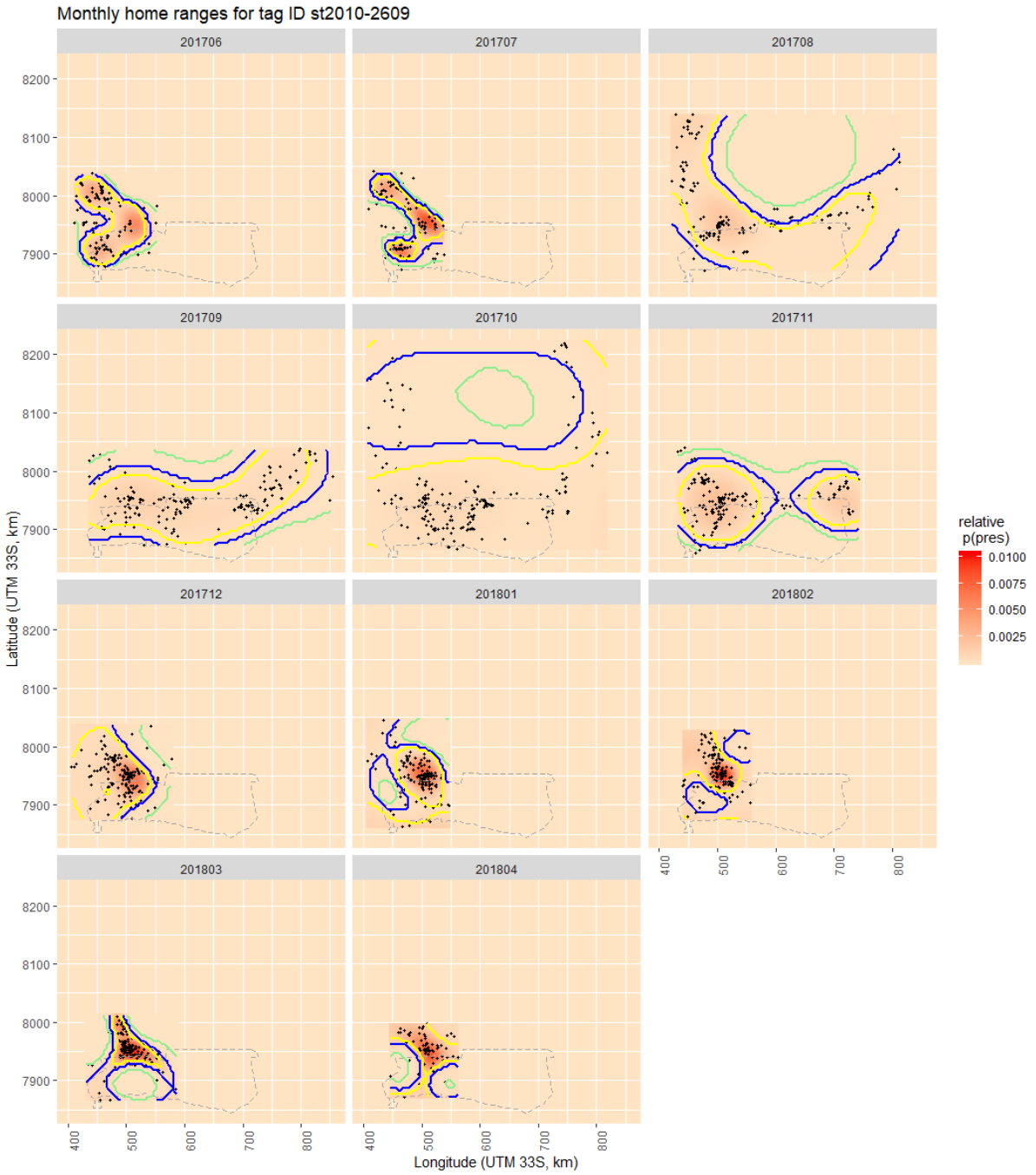

Figure VI. 14 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-2609. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

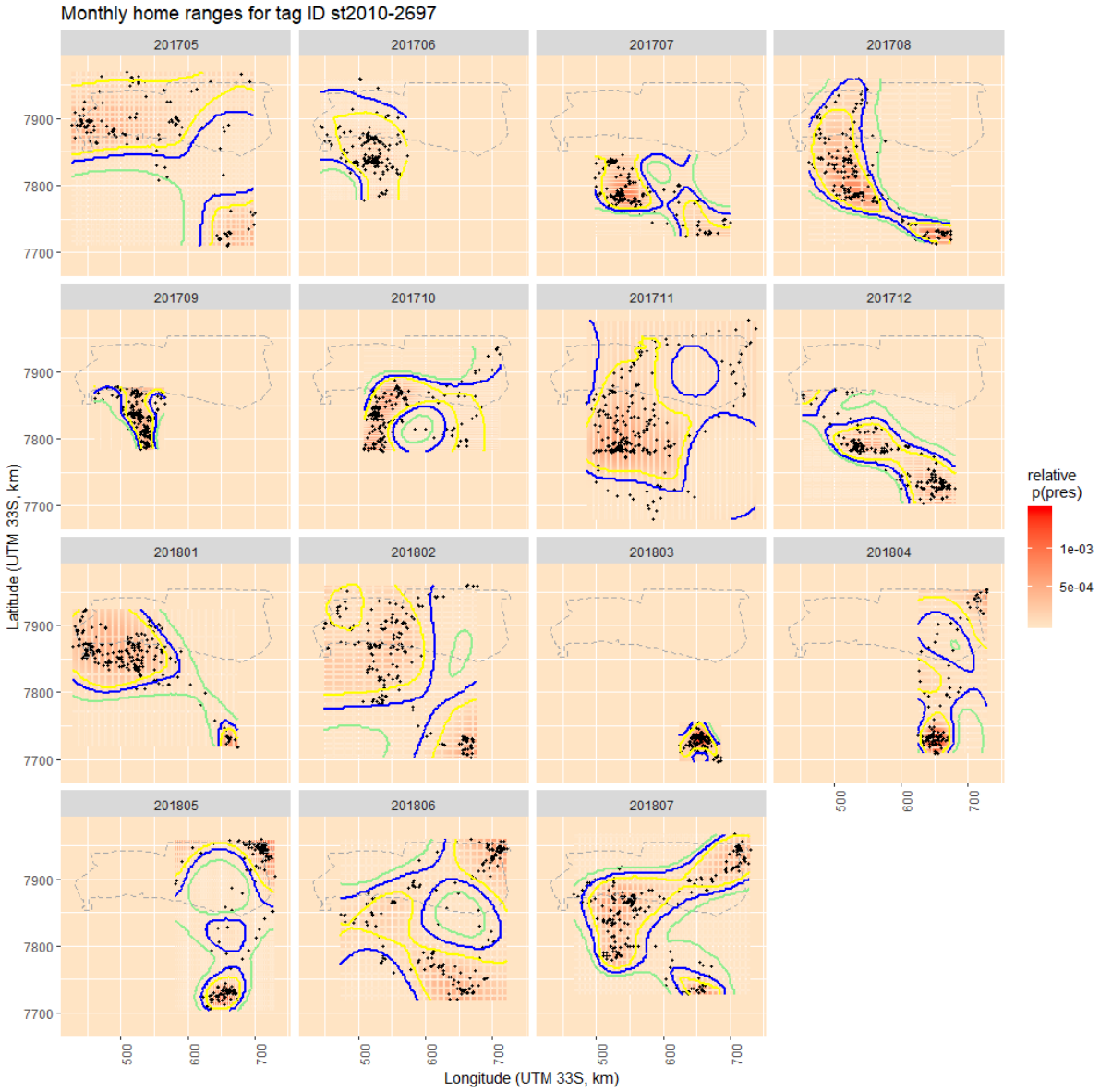

Figure VI. 15 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-2697. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference. The plotting engine in use failed displaying parts of the probability raster.

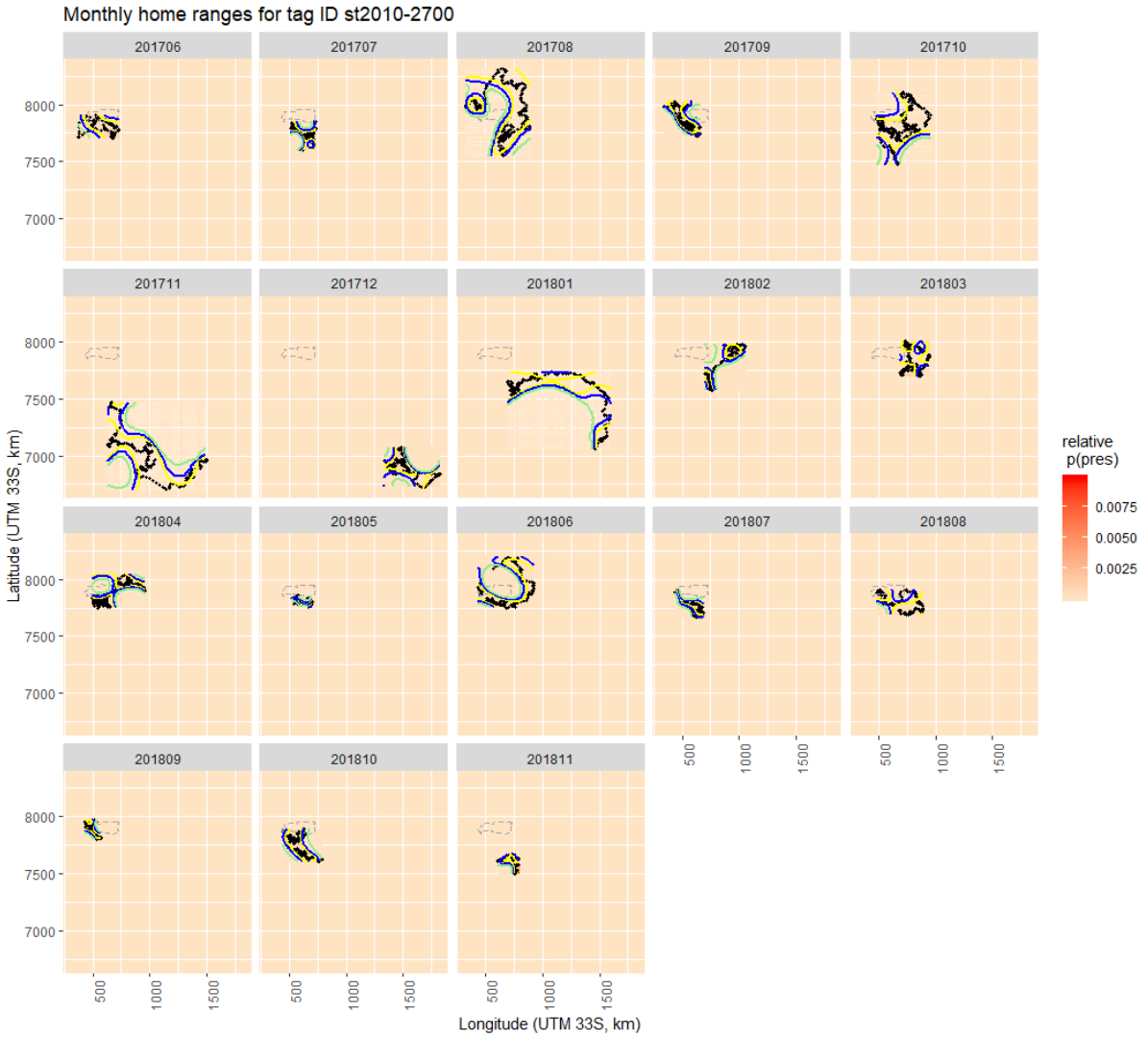

Figure VI. 16 Variation in the mean monthly home range in terms of geographic location, for bird ID st2010-2700. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

Core area

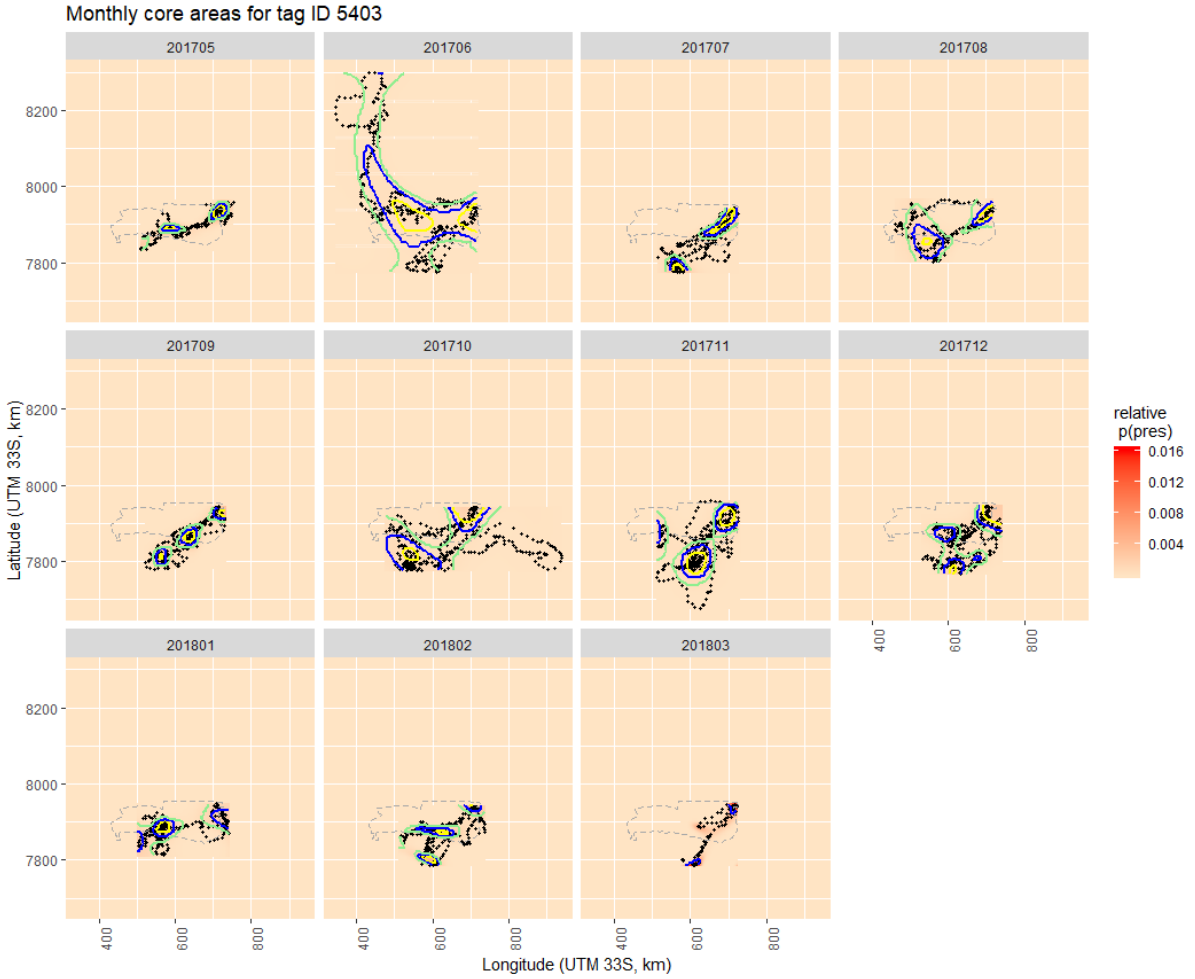

Figure VI. 17 Variation in the mean monthly core area in terms of geographic location, for bird ID 5403. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

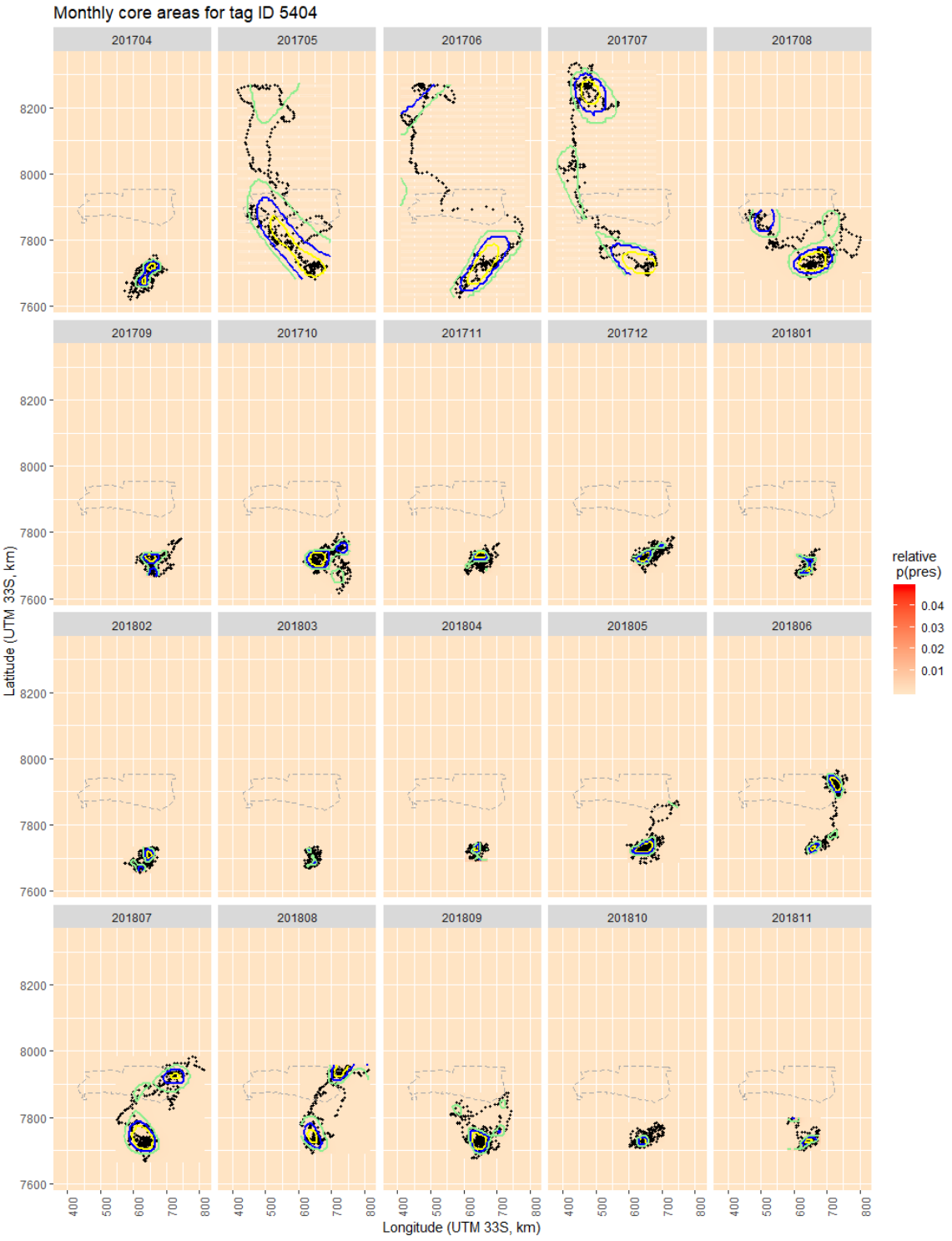

Figure VI. 18 Variation in the mean monthly core area in terms of geographic location, for bird ID 5404. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

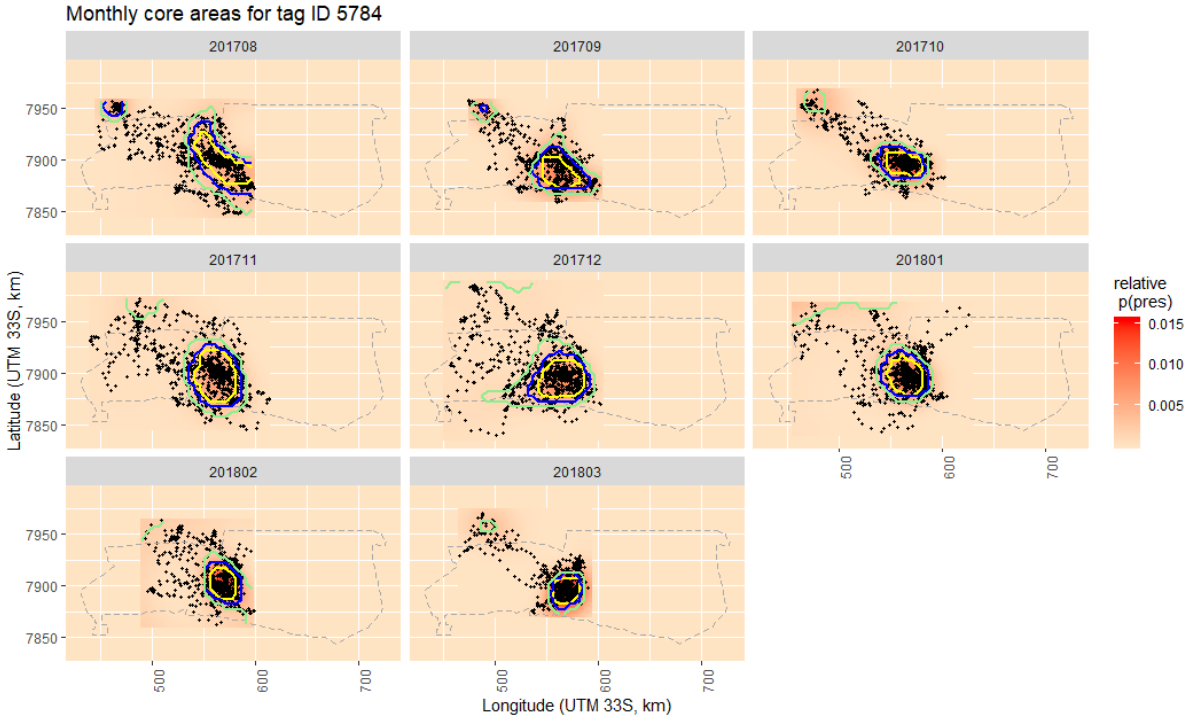

Figure VI. 19 Variation in the mean monthly core area in terms of geographic location, for bird ID 5784. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

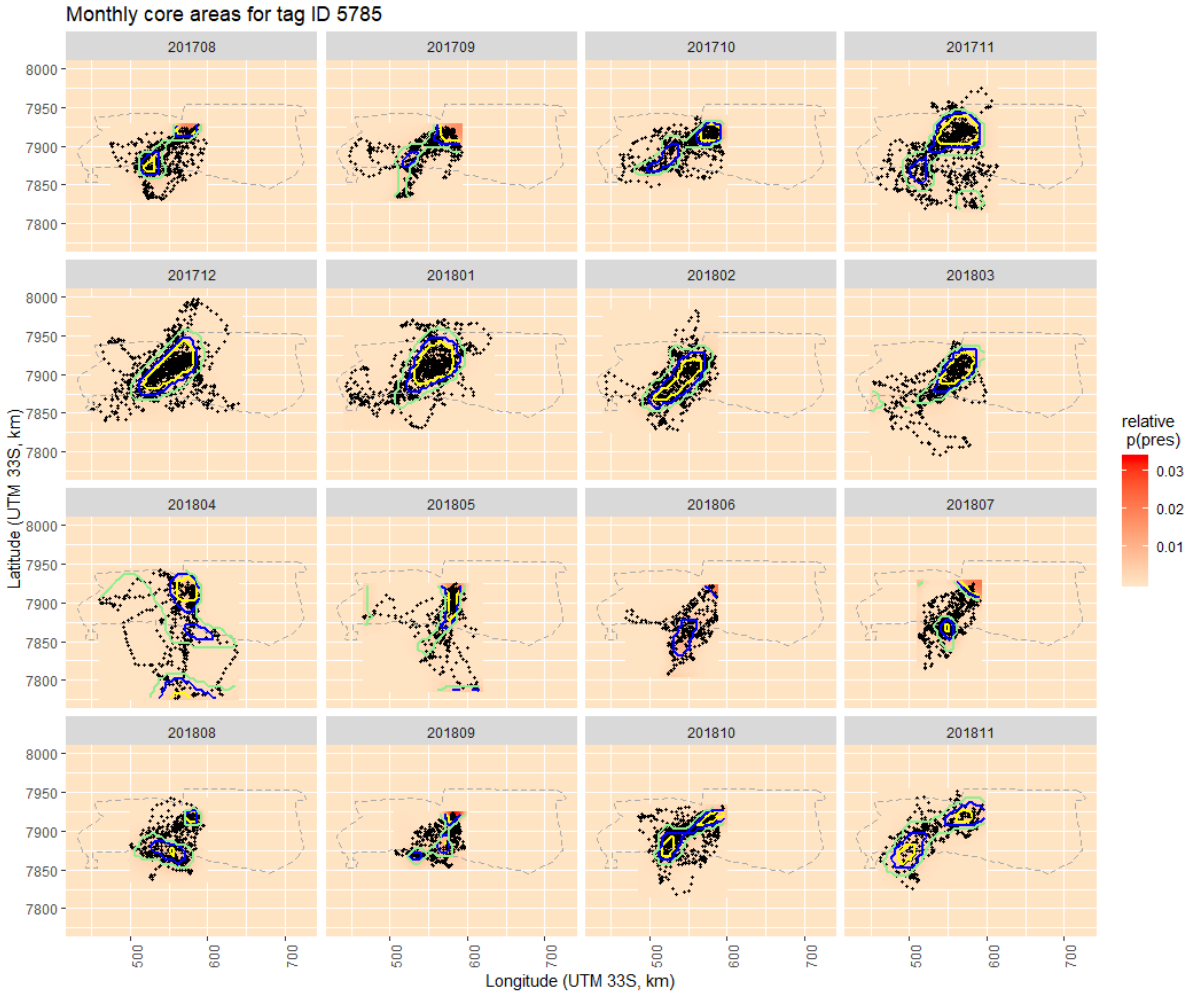

Figure VI. 20 Variation in the mean monthly core area in terms of geographic location, for bird ID 5785. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

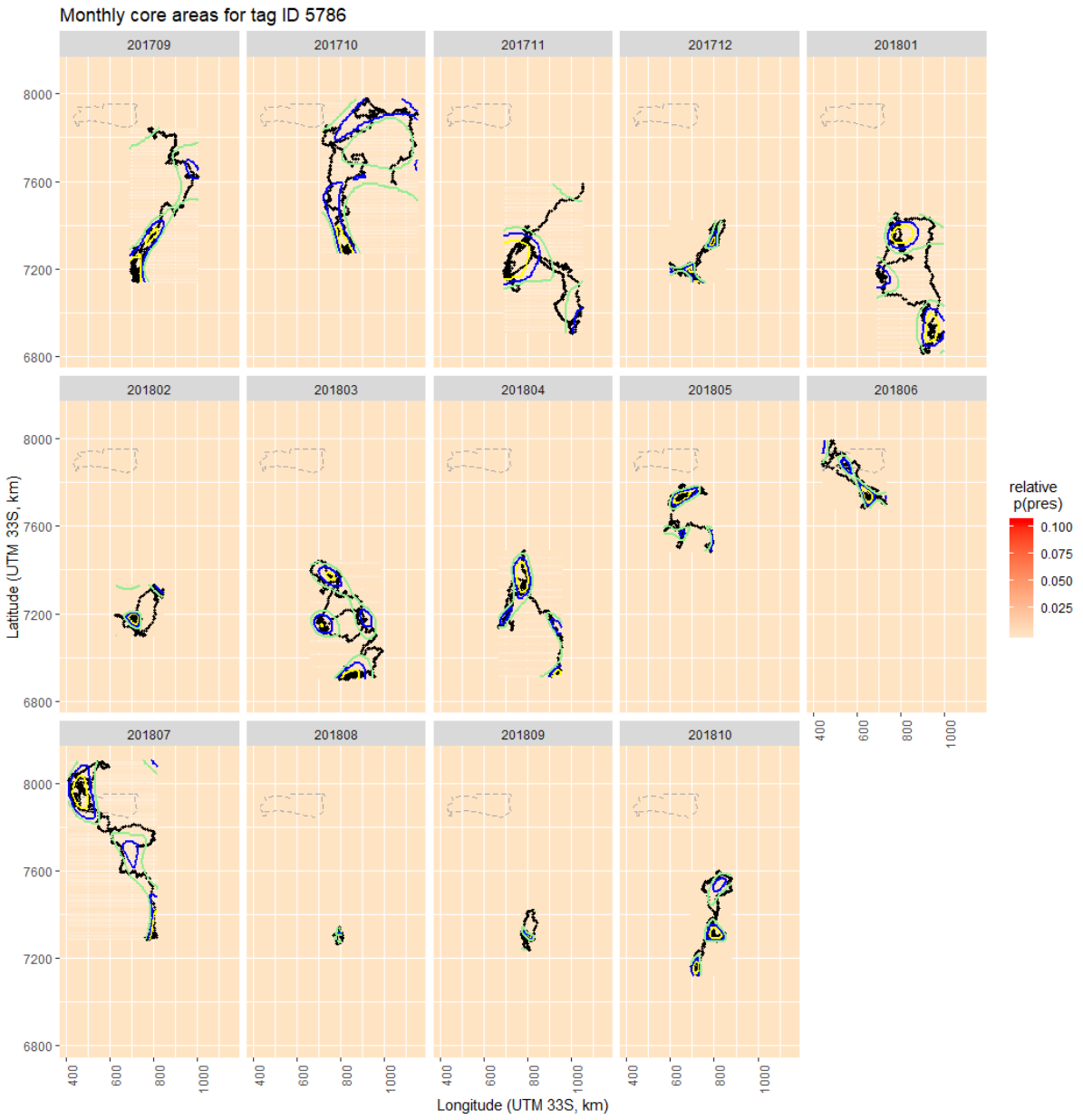

Figure VI. 21 Variation in the mean monthly core area in terms of geographic location, for bird ID 5786. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Park (dashed grey line) shown for reference.

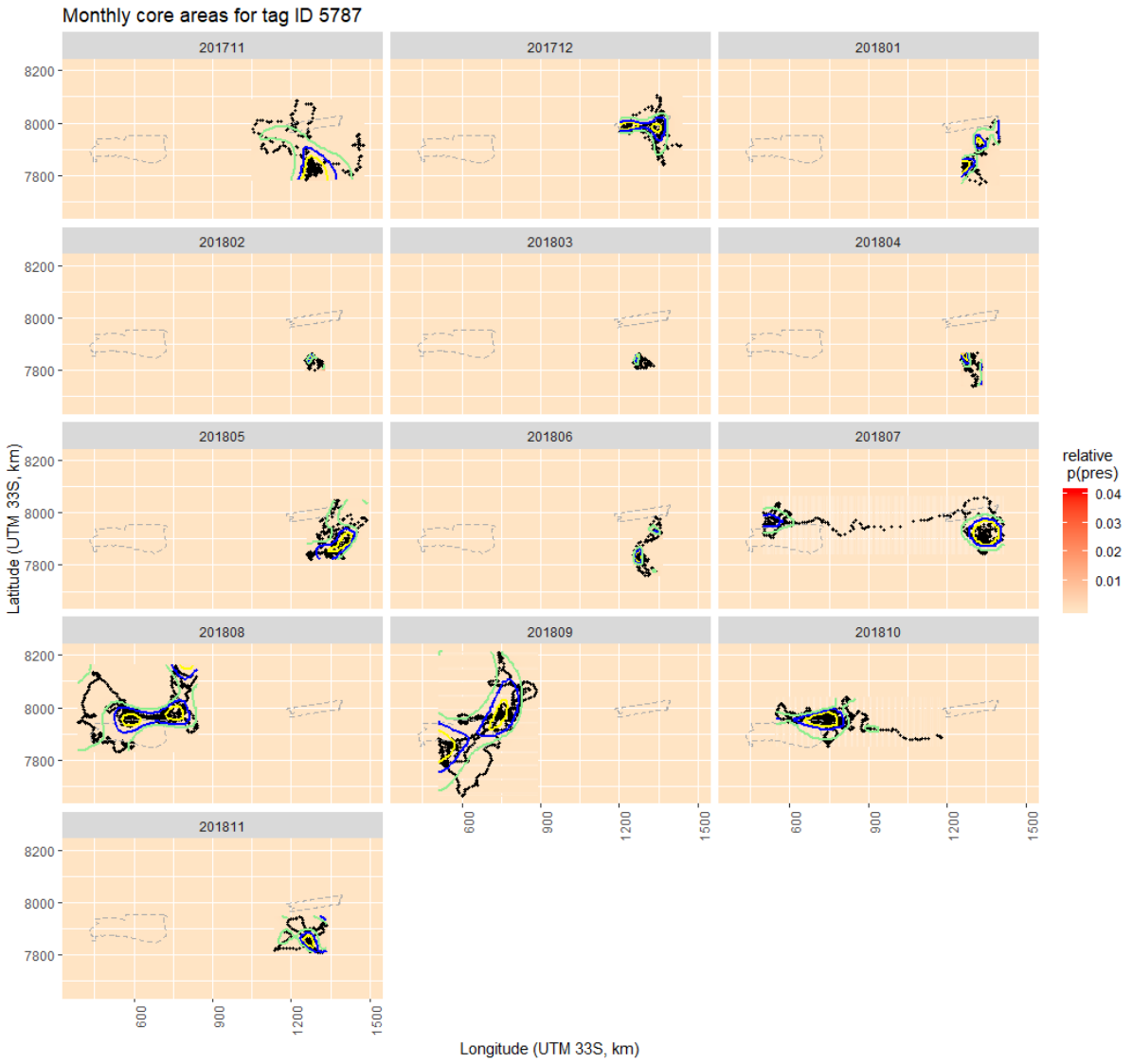

Figure VI. 22 Variation in the mean monthly core area in terms of geographic location, for bird ID 5787. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha and Bwabwata (NE) National Parks (dashed grey line) shown for reference.

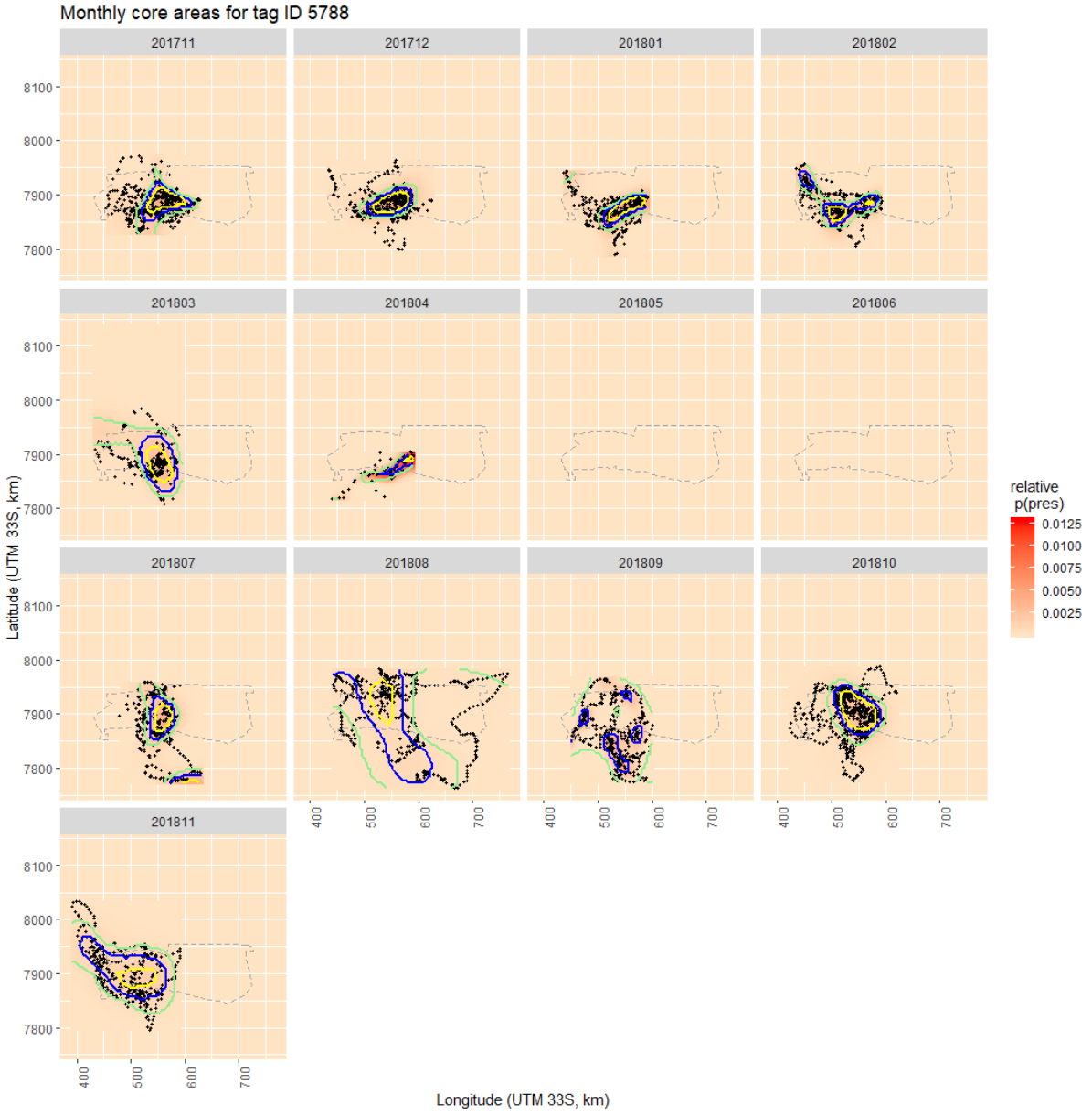

Figure VI. 23 Variation in the mean monthly core area in terms of geographic location, for bird ID 5788. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

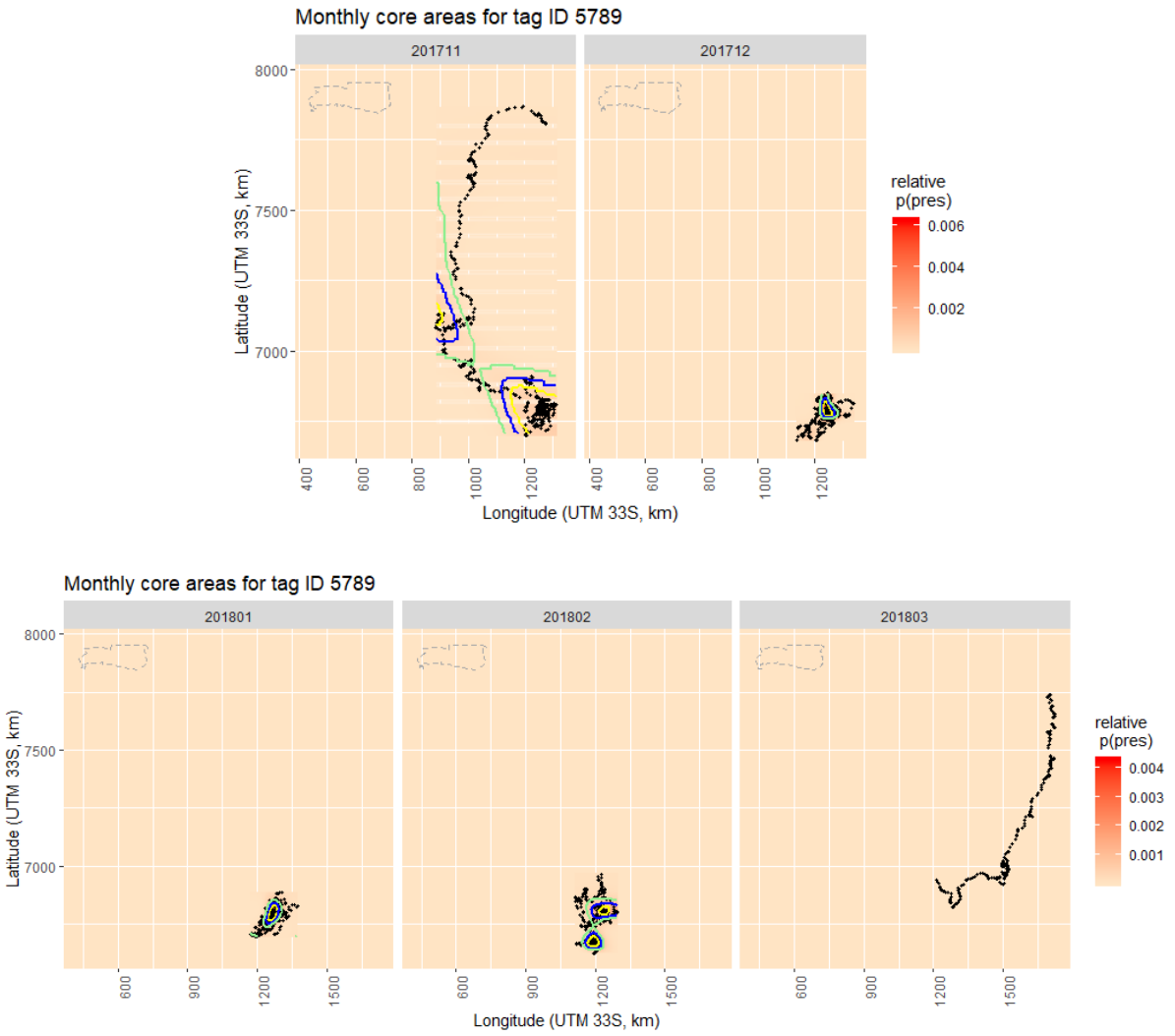

Figure VI. 24 Variation in the mean monthly core area in terms of geographic location, for bird ID 5789. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference. The plotting engine in use failed displaying the contours and parts of the probability raster.

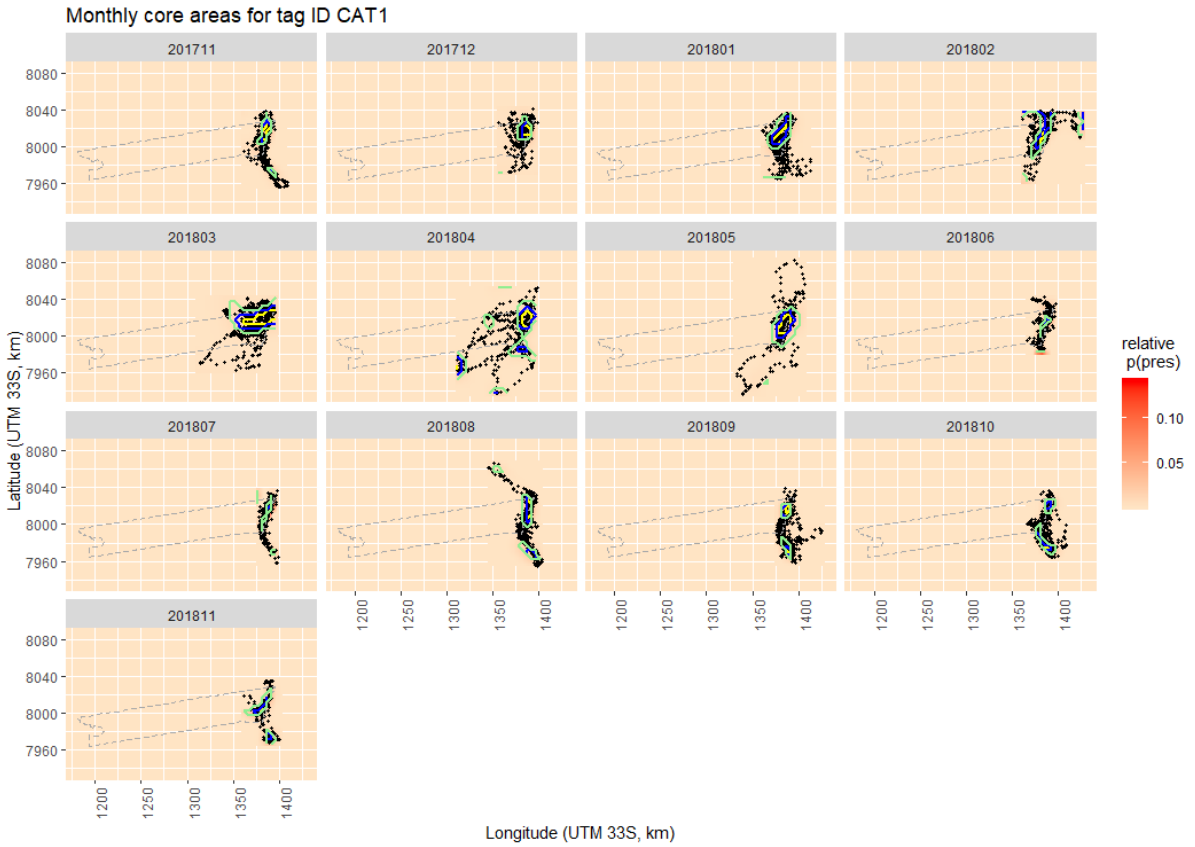

Figure VI. 25 Variation in the mean monthly core area in terms of geographic location, for bird ID CAT1. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Parks (dashed grey line) shown for reference.

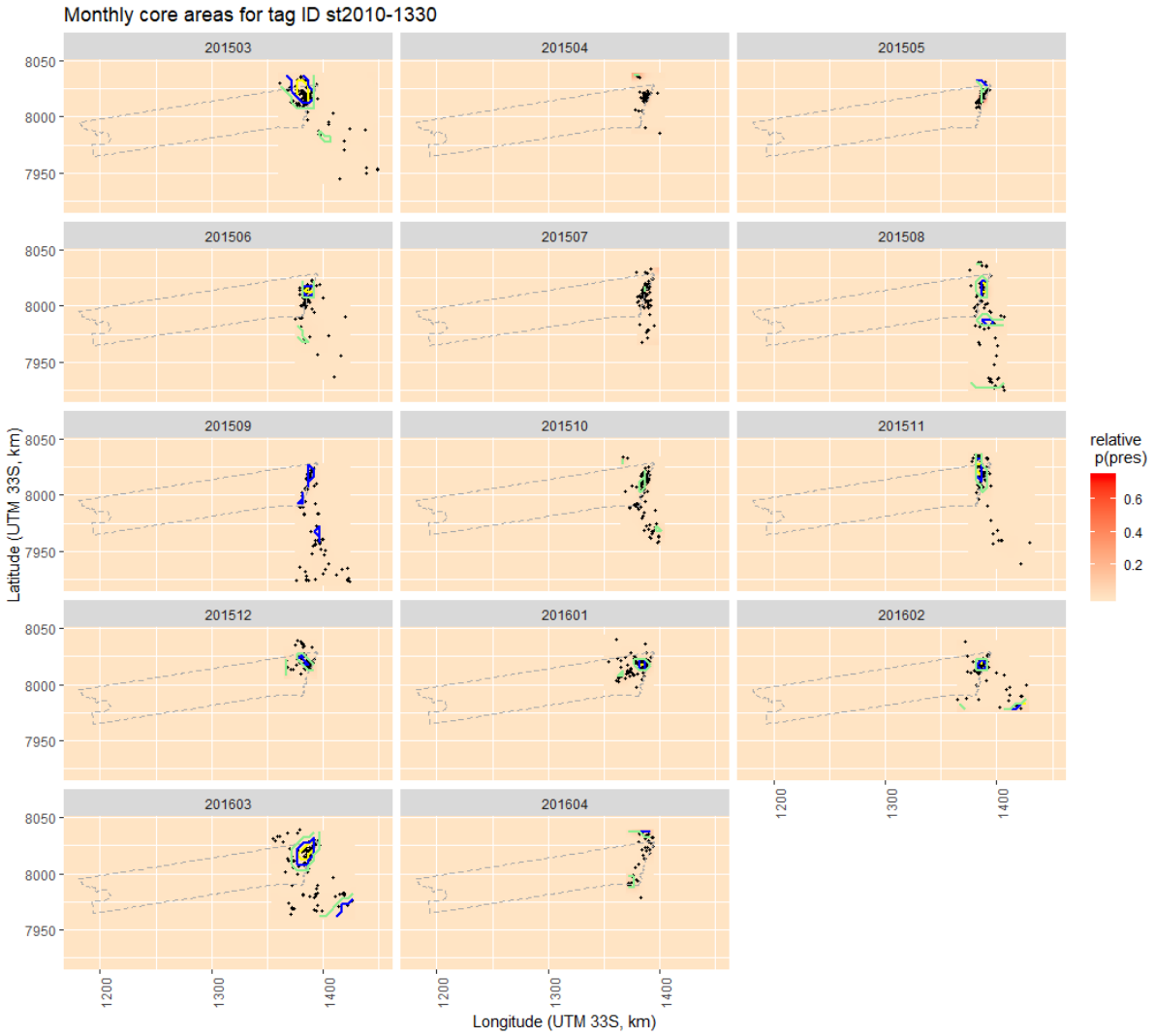

Figure VI. 26 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-1330. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Parks (dashed grey line) shown for reference.

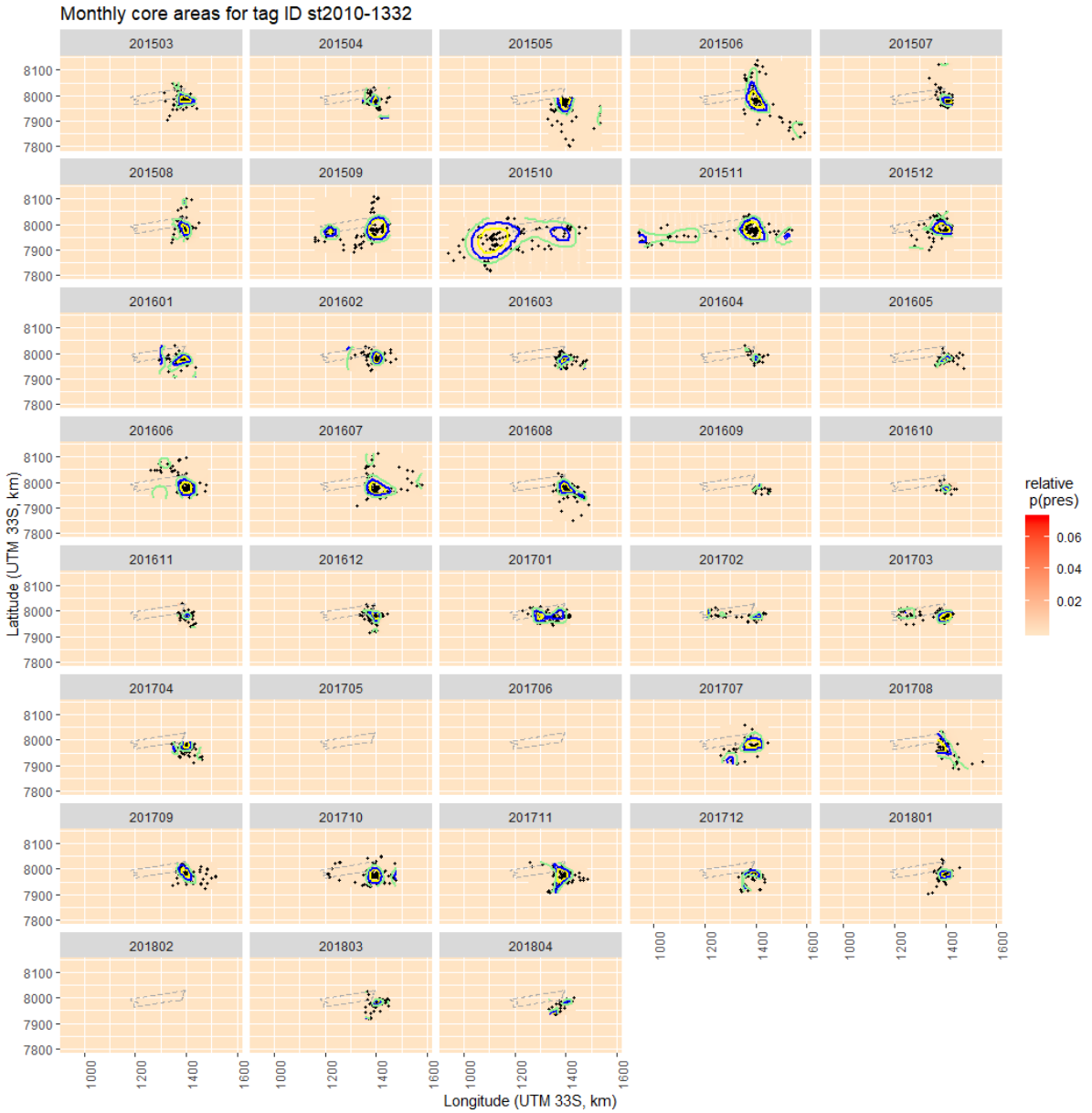

Figure VI. 27 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-1332. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Bwabwata National Parks (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

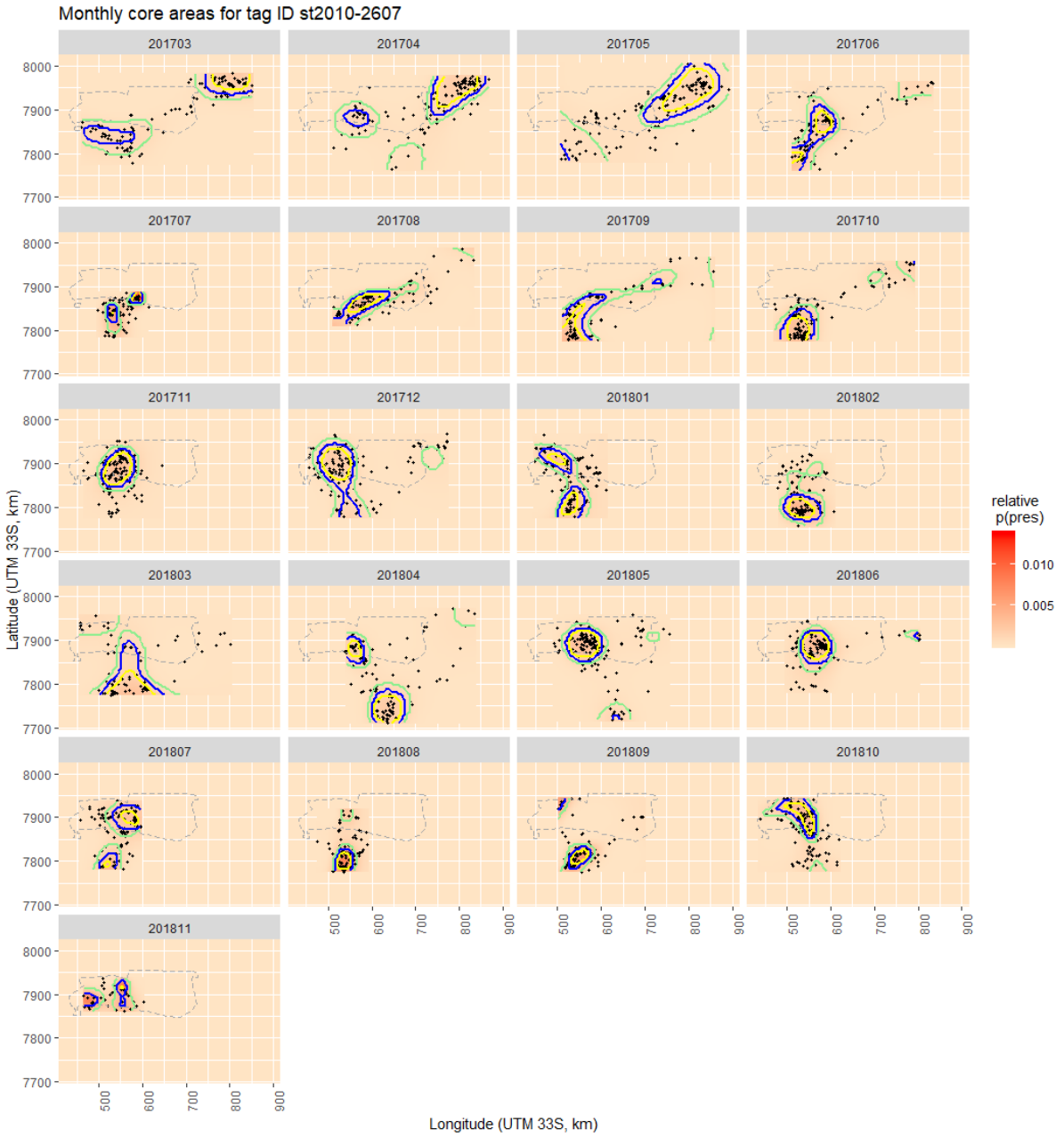

Figure VI. 28 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-2607. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference.

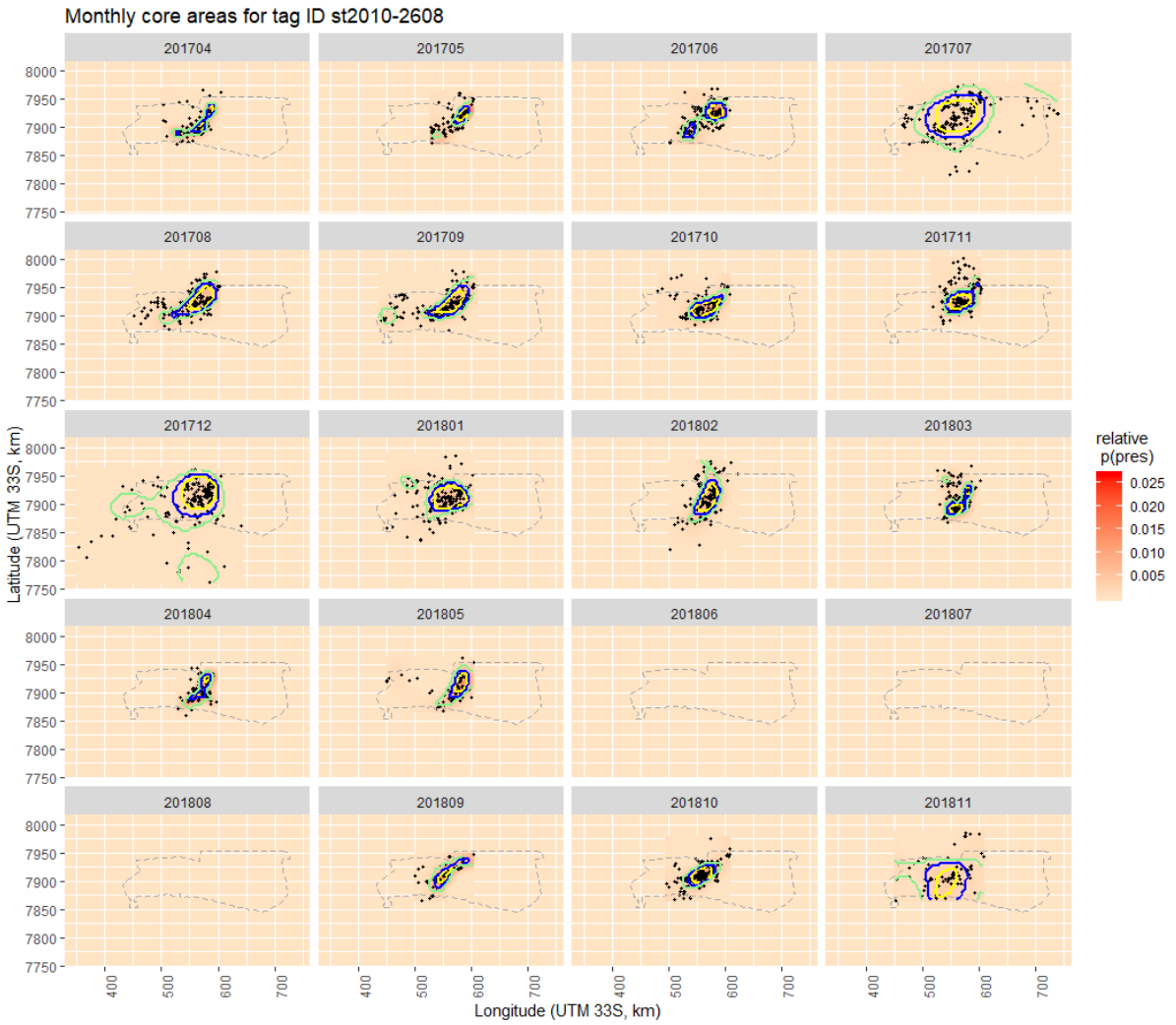

Figure VI. 29 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-2608. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference. Plots shown in blank did not have enough data to generate range areas

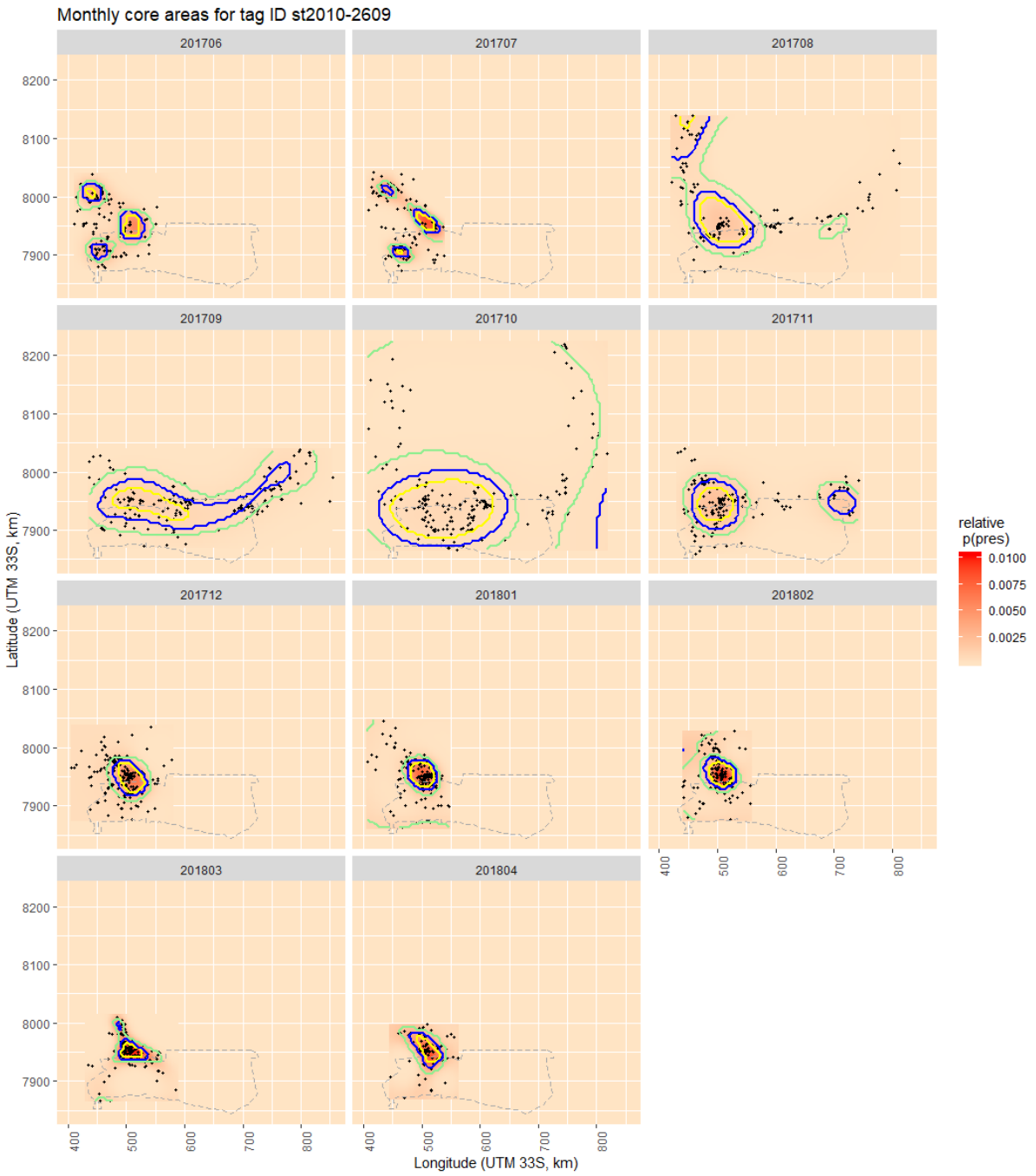

Figure VI. 30 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-2609. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference.

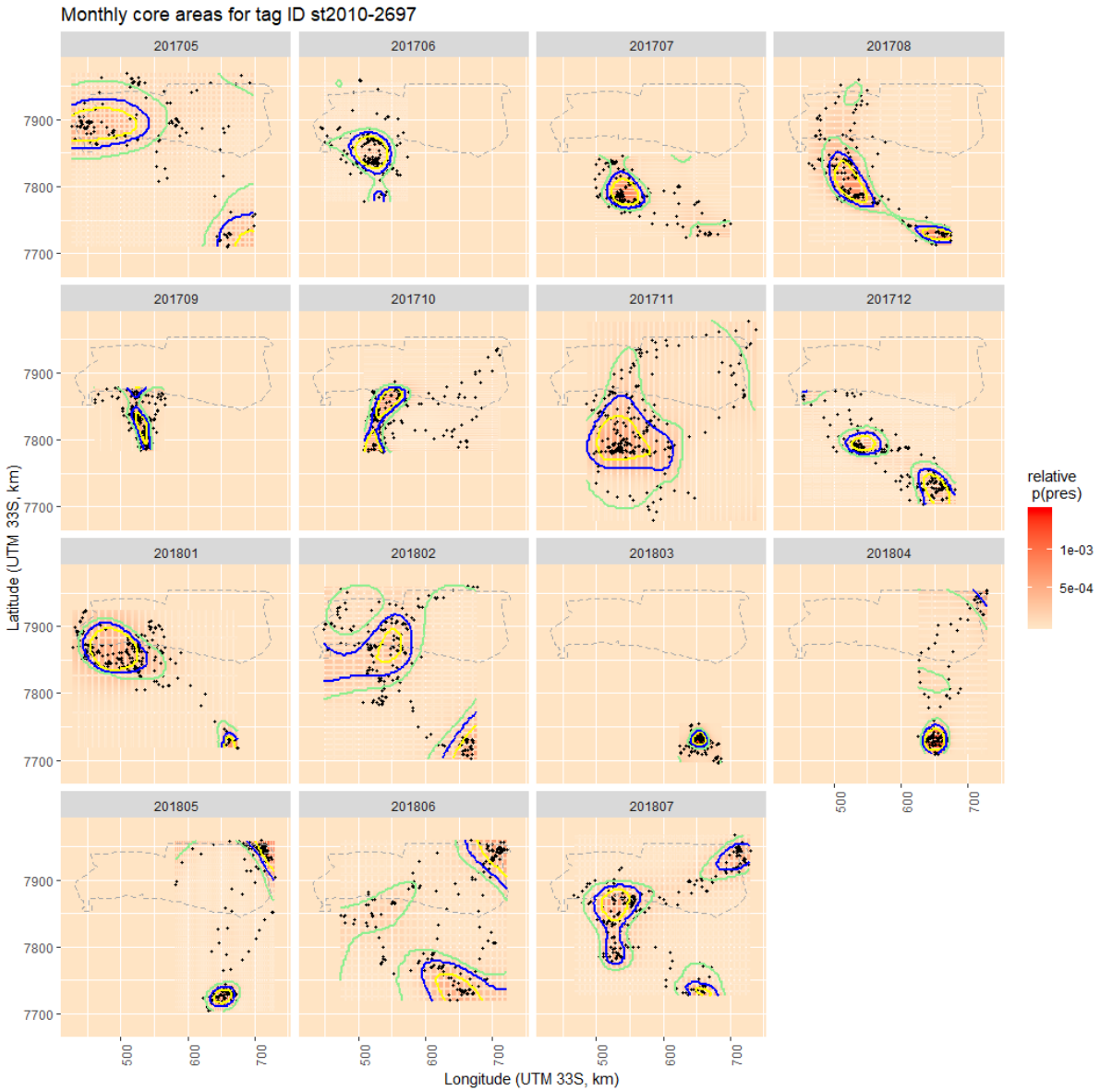

Figure VI. 31 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-2697. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference. The plotting engine in use failed displaying parts of the probability raster.

Figure VI. 32 Variation in the mean monthly core area in terms of geographic location, for bird ID st2010-2700. The relative probabilities of presence (in red gradient) and vulture locations (black dots) are shown. Mean range area contour shown in blue, lower 95% confidence limits shown in yellow, and upper 95% CI shown in green. Borders of Etosha National Parks (dashed grey line) shown for reference.

Appendix VII Habitat modelling: Characterisation of the overall study area

Habitat characteristics

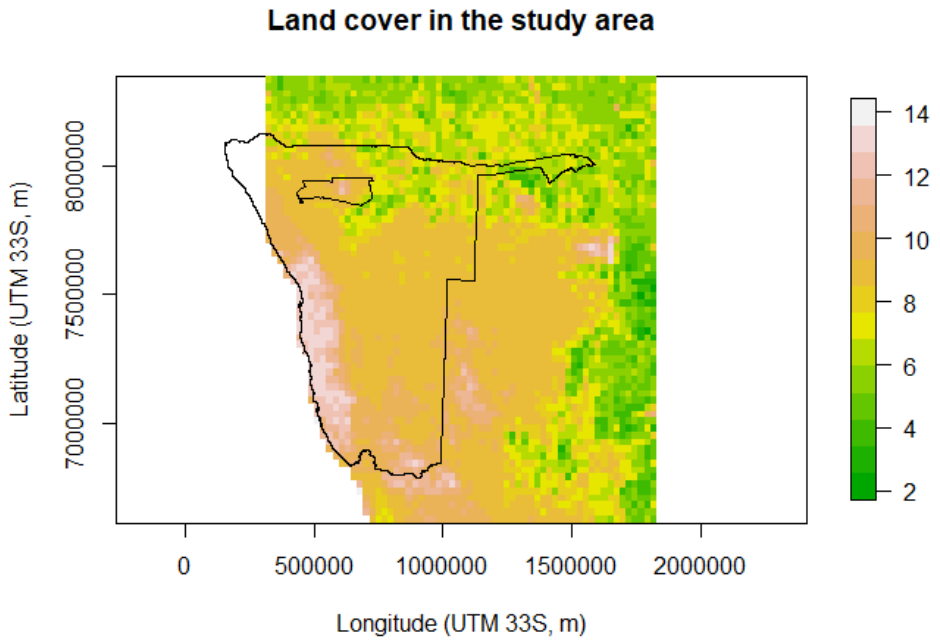

Figure VII. 1 Characterization of the study area in terms of land cover. The 14 GlobCover 2009 land cover classification are as follow: 1. post-flooding or irrigated croplands; 2.rainfed croplands; 3. mosaic cropland (50-70%)/vegetation (grassland, shrubland, forest) (20-50%); 4. mosaic vegetation (grassland, shrubland, forest) (50-70%) / Cropland (20-50%); 5. closed to open (>15%) broadleaved evergreen and/or semi-deciduous forest (>5m); 6. closed (>40%) broadleaved deciduous forest (>5m); 7. open (15-40%) broadleaved deciduous forest (>5m); 8. closed (>40%) needle-leaved evergreen forest (>5m); 9. open (15-40%) needle-leaved deciduous or evergreen forest (>5m); 10. closed to open (>15%) mixed broadleaved and needle-leaved forest (>5m); 11. mosaic forest/shrubland (50-70%)/grassland (20-50%); 12. mosaic grassland (50-70%)/forest/shrubland (20-50%); 13. closed to open (>15%) shrubland (<5m); 14. closed to open (>15%) grassland; 15. sparse (>15%) vegetation (woody vegetation, shrubs, grassland); 16. closed (>40%) broadleaved forest regularly flooded (fresh water); 17. closed (>40%) broadleaved semi-deciduous and/or evergreen forest regularly flooded (saline water); 18. closed to open (>15%) vegetation (grassland, shrubland, woody vegetation) on regularly flooded or waterlogged soil (fresh, brackish or saline water); 19. artificial surfaces and associated areas (urban areas >50%); 20. bare areas; 21. water bodies; 22. permanent snow and ice. The borders of Namibia and the Etosha National park shown for reference.

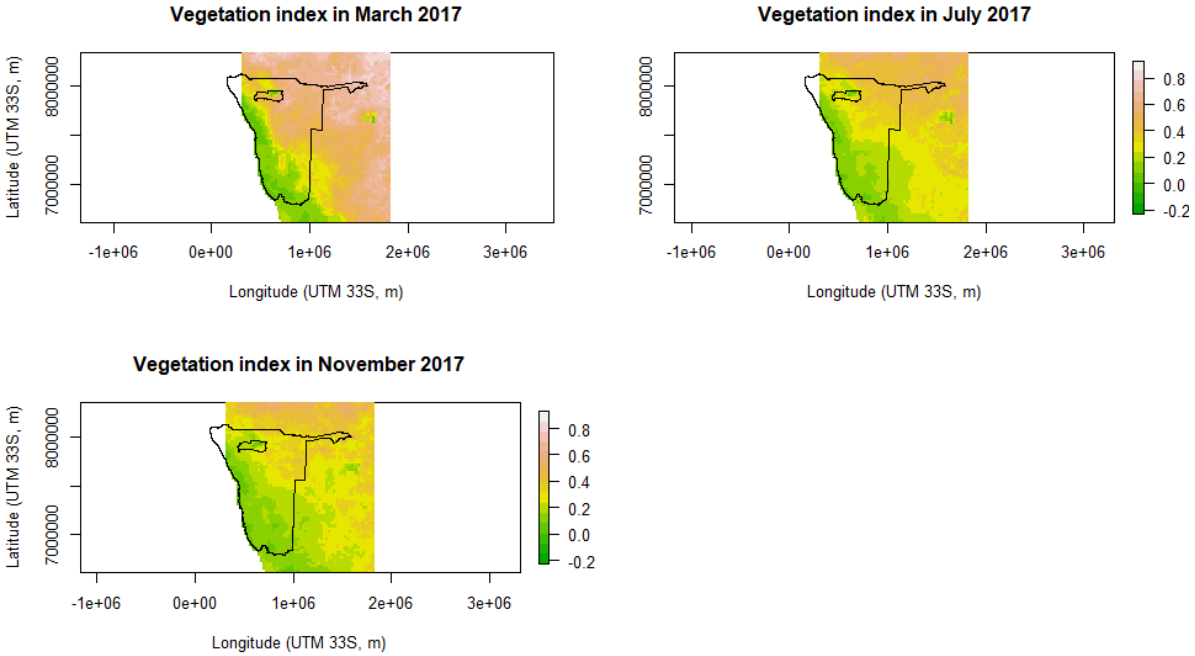

Figure VII. 2 Average vegetation index (represented by the normalized difference vegetation index, NDVI) in each grid cell over the study area, for each representative month of each season considered in the present study (March for the hot wet season, July for cold dry, and November for small rain). Border of Namibia shown for context.

Figure VII. 3 Seven main rivers in Southern Africa and boundary of the study area. These rivers may take distinct names in different countries or regions and are: Cunene (Angola), Kunene (Namibia); Cubango (Angola), Okavango (Namibia, Botswana); Cuito (Angola, and Khwai river in Botswana); Cuando (Angola), Chobe and Linyanti (Namibia), Kwando (Botswana); Zambezi (Namibia, Zimbabwe, Zambia, and Botswana); Limpopo (Zimbabwe, Botswana), and Orange (Namibia, South Africa also with Vaal river).

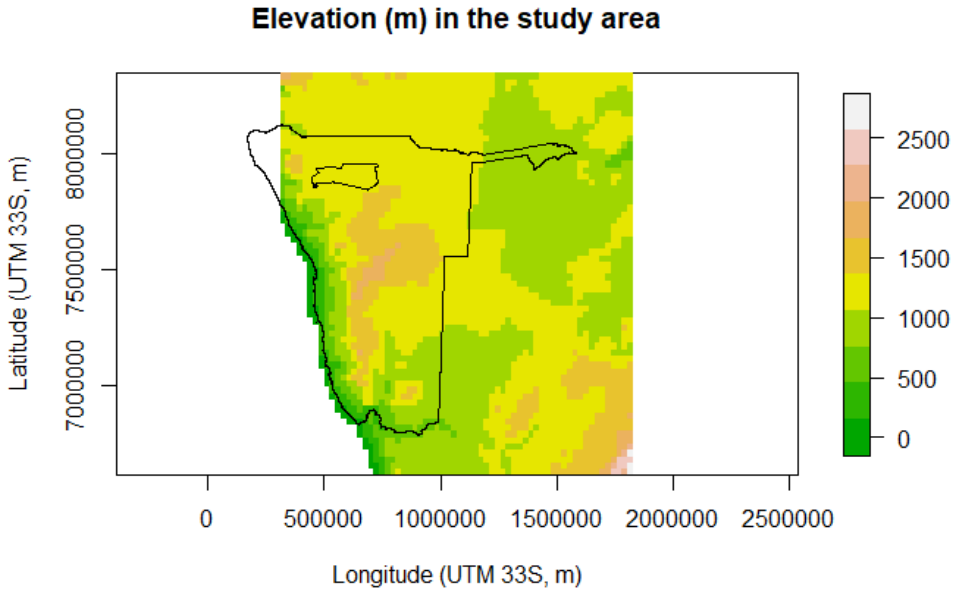

Figure VII. 4 Average elevation (m) in each grid cell over the study area. Border of Namibia shown for context.

Climate variables

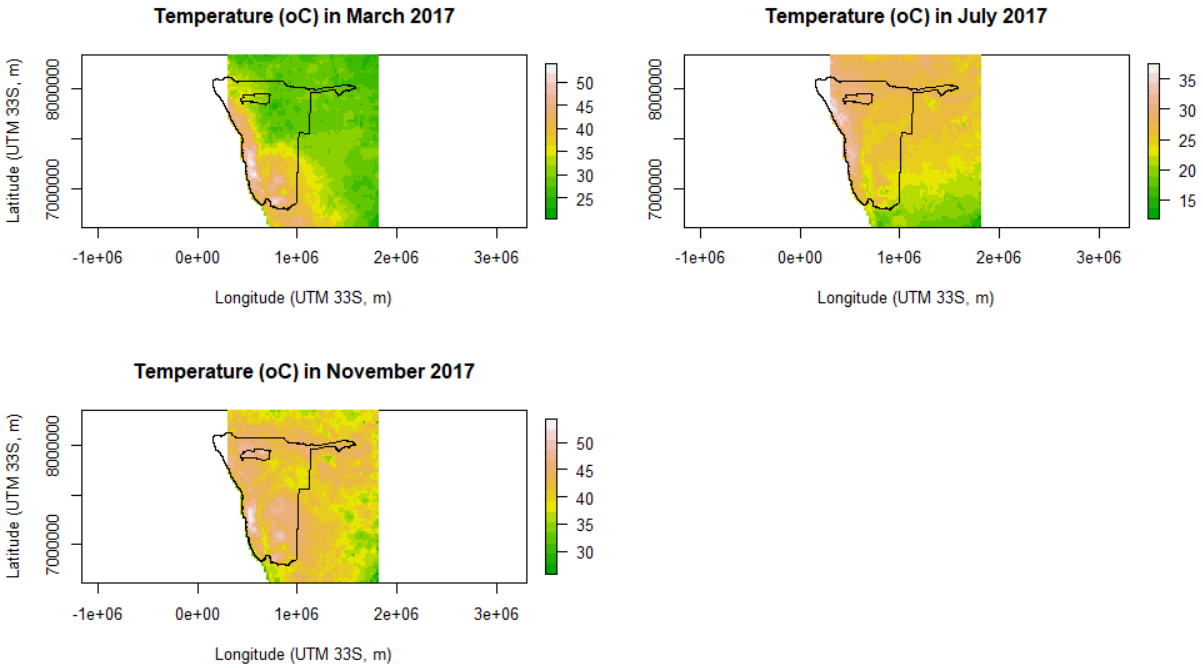

Figure VII. 5 Average temperature (°C) in each grid cell over the study area, for each representative month of each season considered in the present study (March for the hot wet season, July for cold dry, and November for small rain). Note each map has its own scaling to allow better detail in July. Border of Namibia shown for context.

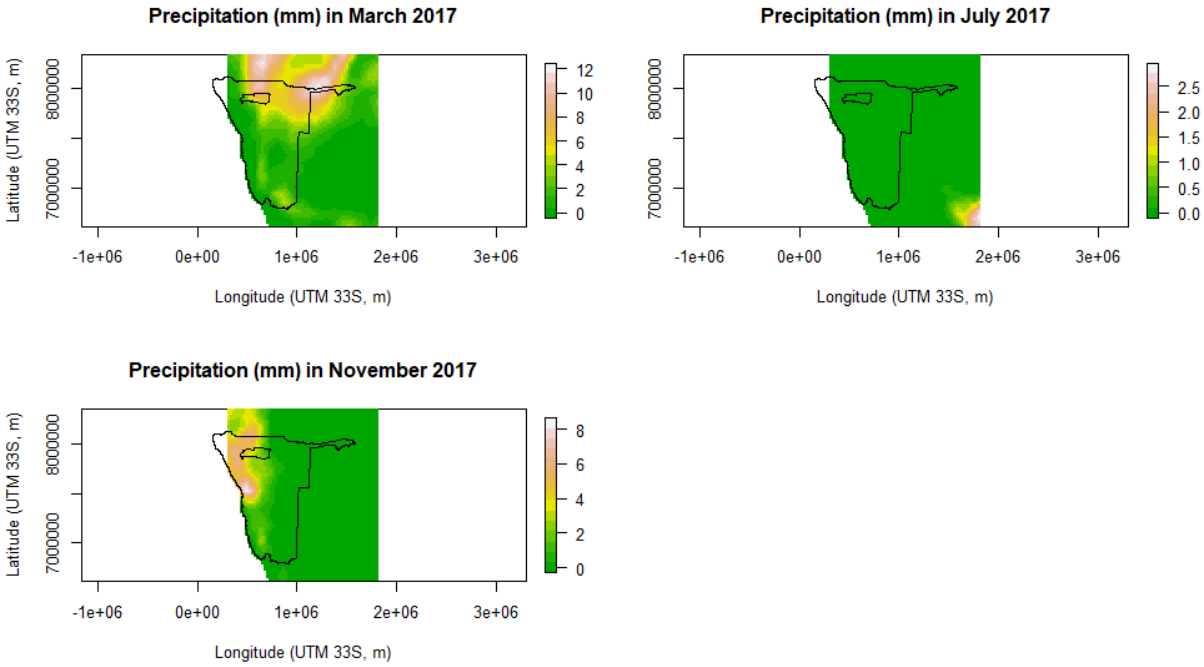

Figure VII. 6 Average precipitation (mm) in each grid cell over the study area, for each representative month of each season considered in the present study (March for the hot wet season, July for cold dry, and November for small rain). Note each map has its own scaling to allow better detail. Border of Namibia shown for context.

Human presence

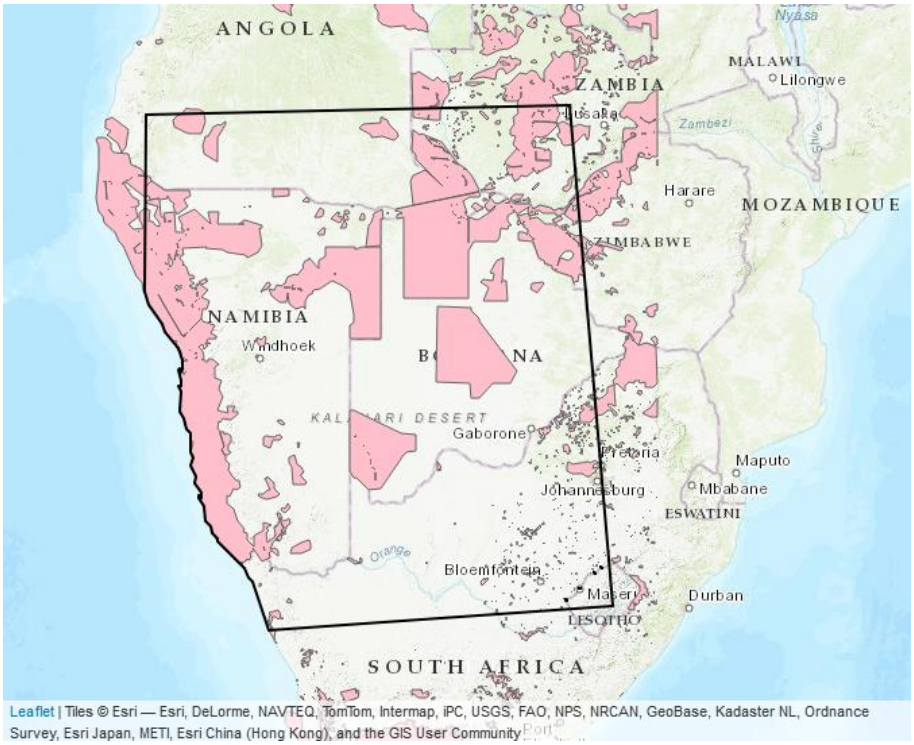

Figure VII. 7 Areas with some level of protection in Southern Africa and boundary of the study area.

Further details on Protected areas

Accepted Values	Description[3]
Ia	*Strict Nature Reserve*
● Ib	*Wilderness area*
● II	*National Park*
● III	*Natural Monument or feature*
● IV	*Habitat/species management area*
● V	*Protected landscape/seascape*
● VI	*Protected area with sustainable use of natural resources*
● Not Reported	For protected areas where an IUCN category is unknown and/or the data provider has not provided any related information.
● Not Applicable	The IUCN Management Categories are not applicable to a specific designation type. This currently applies to World Heritage Sites and UNESCO MAB Reserves. Not Applicable also applies to a site that does not fit the standard definition of a protected area (PA_DEF field = 0).
Not Assigned	The protected area meets the standard definition of protected areas (PAF_DEF = 1) but the data provider has chosen not to use the IUCN Protected Area Management Categories.

Table VII. 1 Description of the International Union for Conservation of Nature (IUCN) management categories used in the classification of protected areas, according to the World Database on Protected Areas [171]. The blue dots signal the categories present in the study area.

Table VII. 2 Description of the ownership type categories used in the classification of protected areas, according to the World Database on Protected Areas [171]. The blue dots signal the categories present in the study area.

Ownership type is often independent of governance and management structures.
It is the individual, organization or group that holds legal or customary ownership or tenure of the land under management.

Accepted Values	Description
State	Owned by the state
Communal	Under communal ownership
Individual landowners	Owned/leased by individual landowners
For-profit organisations	Owned/leased by for-profit organisations
Non-profit organisations	Owned/leased by non-profit organisations
Joint ownership	Under joint ownership
Multiple ownership	Under multiple ownership
Contested	Ownership is contested
Not Reported	When ownership type is not known or given by the data provider

Table VII. 3 Description of the governance type categories used in the classification of protected areas, according to the World Database on Protected Areas [171]. The blue dots signal the categories present in the study area.

Governance is a description of the decision-making structure of a protected area and should describe where the decision-making power of delegating management authority rests. The information provided on governance conforms to the IUCN Governance types described in the IUCN Governance of Protected Areas guidelines[6]. IUCN distinguishes four broad protected area governance types, each with several sub-types (see table below) making a total of 11 types that can be reported to the WDPA.

Accepted Values (Governance subtype)	Description	Governance Type
Federal or national ministry or agency	National Agency in charge.	Governance by Government
Sub-national ministry or agency	Regional, provincial, or municipal agency in charge	
Government-delegated management	Management delegated to another organization (e.g. to Non-governmental Organizations)	
Transboundary governance	Formal arrangements between one or more sovereign States or Territories.	Shared Governance
Collaborative governance	When governance is through various ways in which diverse actors and institutions work together.	
Joint governance	For example, pluralist board or other multi-party governing body.	
Individual landowners	Land under the governance of one legal person.	Private Governance
Non-profit organisations	For example, Non-governmental Organizations or Universities.	
For-profit organisations	For example, corporate landowners.	
Indigenous peoples	Areas under the governance of indigenous peoples	Governance by Indigenous Peoples and Local Communities
Local communities	Areas under the governance of local communities	
Not Reported	When Governance Type is not known or not given	

[6]Borrini-Feyerabend et al. (2013). Governance of Protected Areas: From understanding to action. Best Practice Protected Area Guidelines Series No. 20, Gland, Switzerland: IUCN.

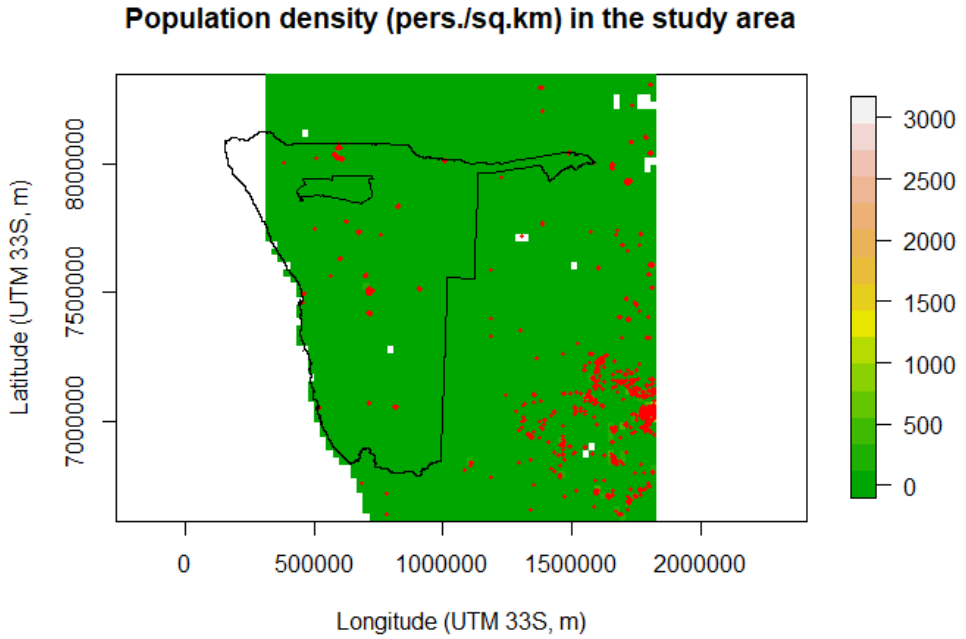

Figure VII. 8 Average population density (persons/sw.km) in each grid cell over the study area. Point in red show areas with more than 100 persons/sq.km. Border of Namibia shown for context.

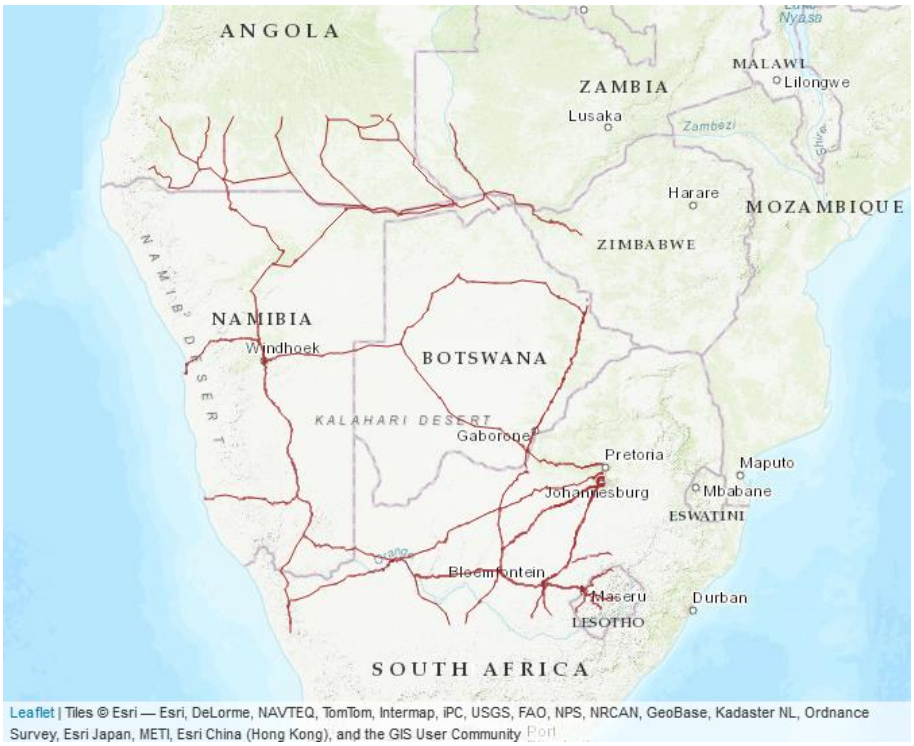

Figure VII. 9 Main roads within the study area. Forty-three roads are shown: EN- roads in Angola (100, 110, 120, 140, 160, 170, 180, 280, 295), M10 in Zambia, A8 in Zimbabwe, A- roads in Botswana (1 to 3) and in Lesotho (1 to 5), N-roads in South Africa (1 to 18) and B- roads in Namibia (1 to 8, except 5 and 7).

Appendix VIII Habitat modelling: functional responses for each vulture

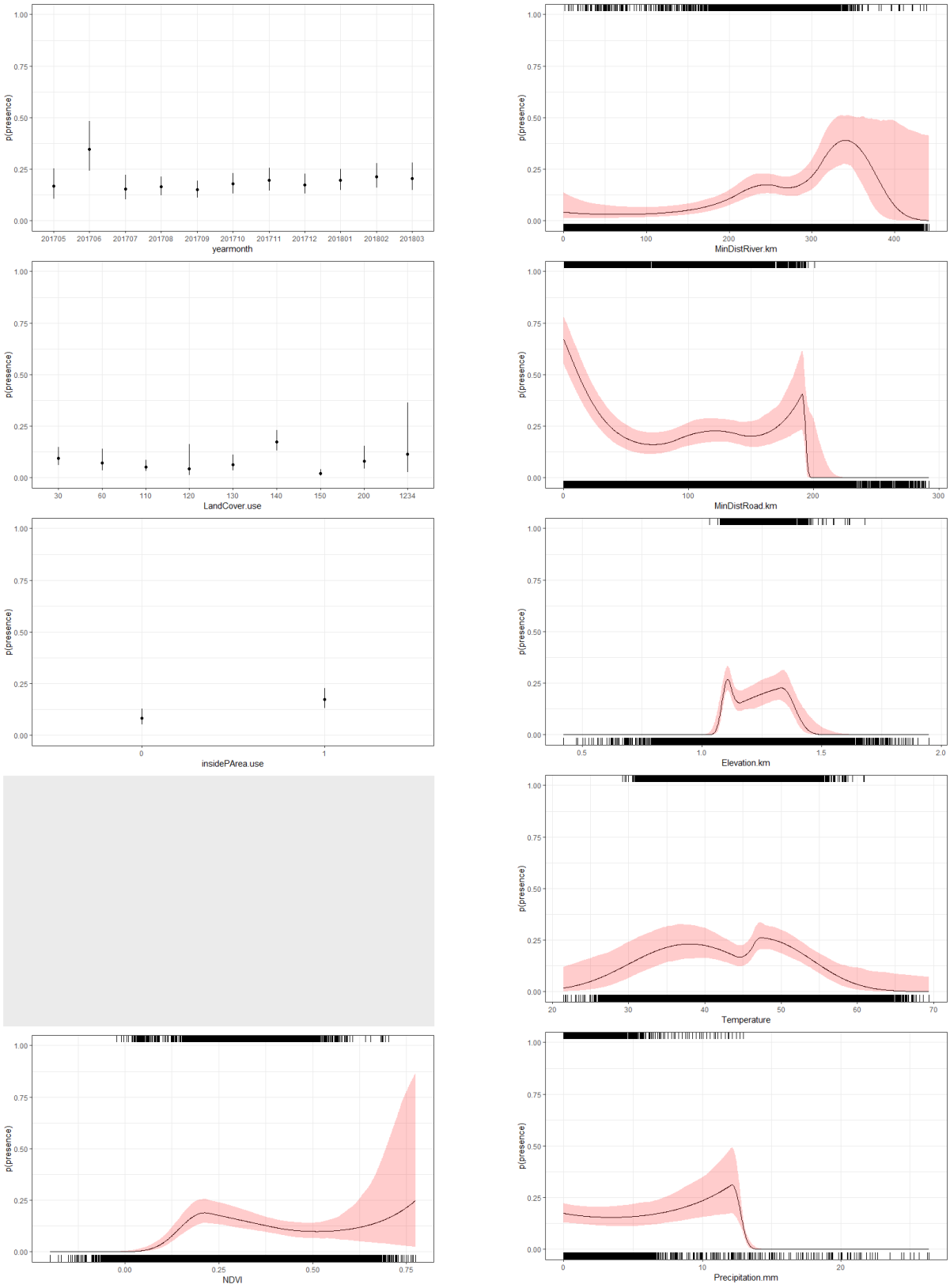

Figure VIII. 1 Functional response for each model covariate for bird 5403. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

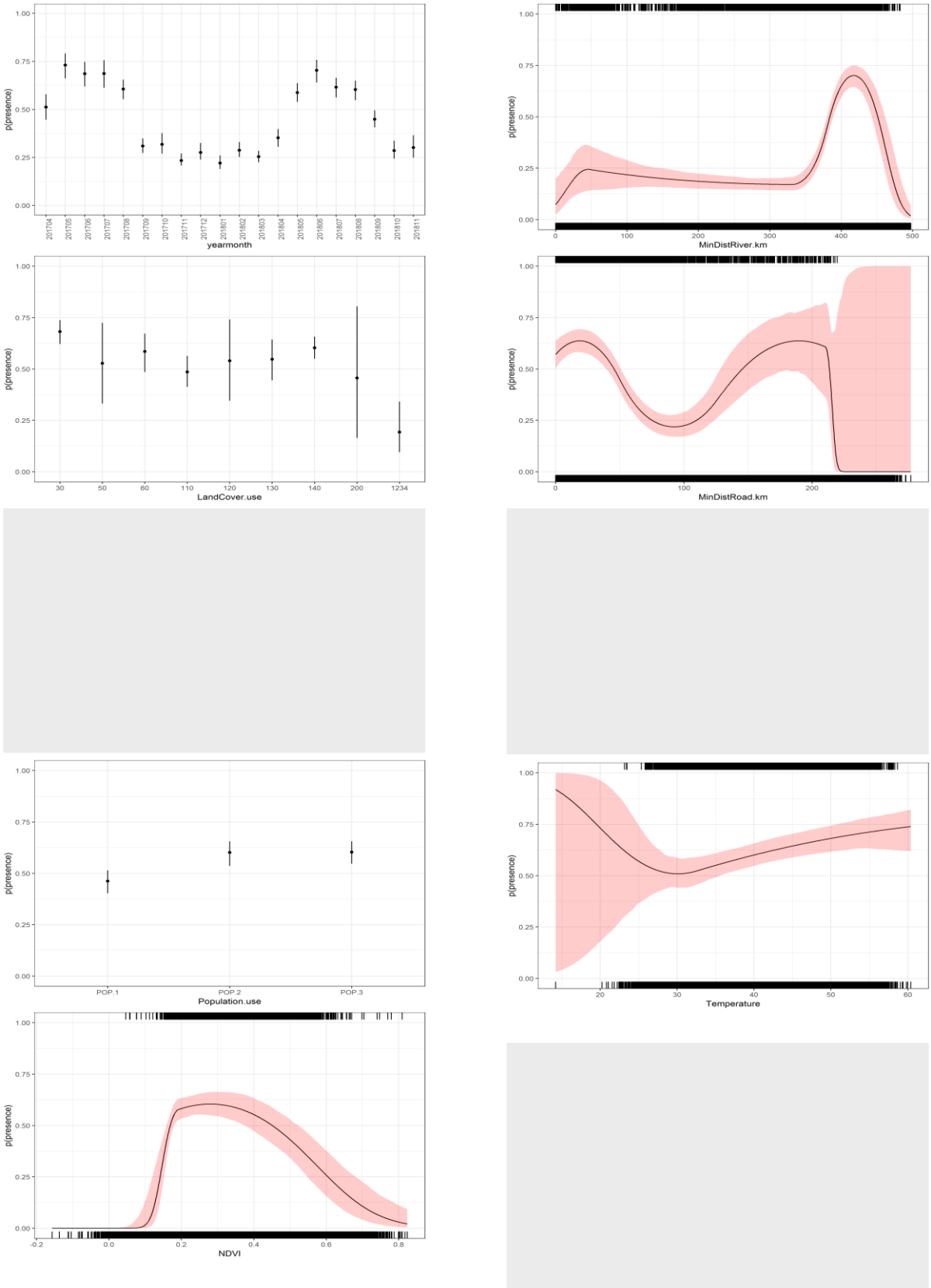

Figure VIII. 2 Functional response for each model covariate for bird 5404. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

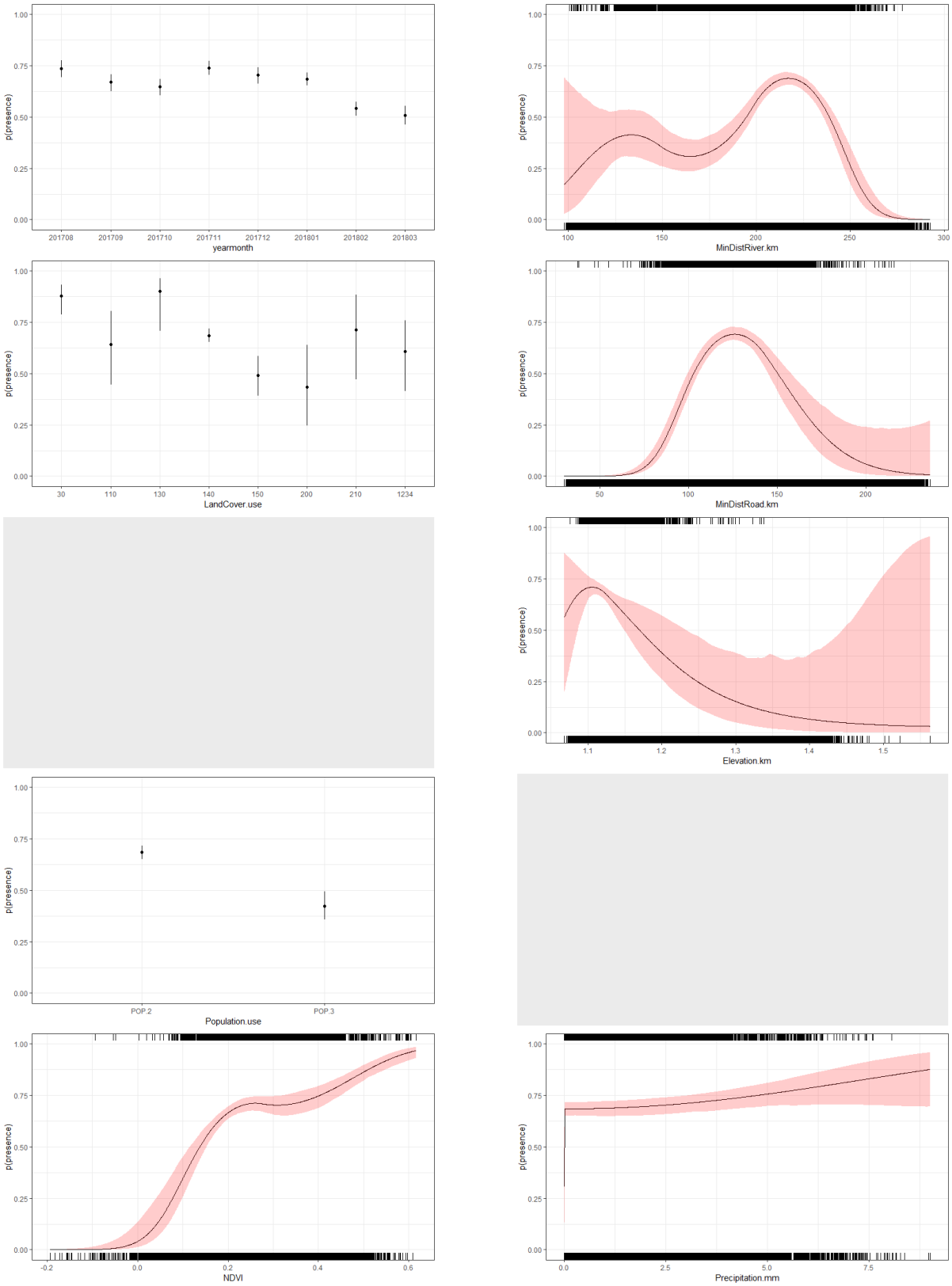

Figure VIII. 3 Functional response for each model covariate for bird 5784. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

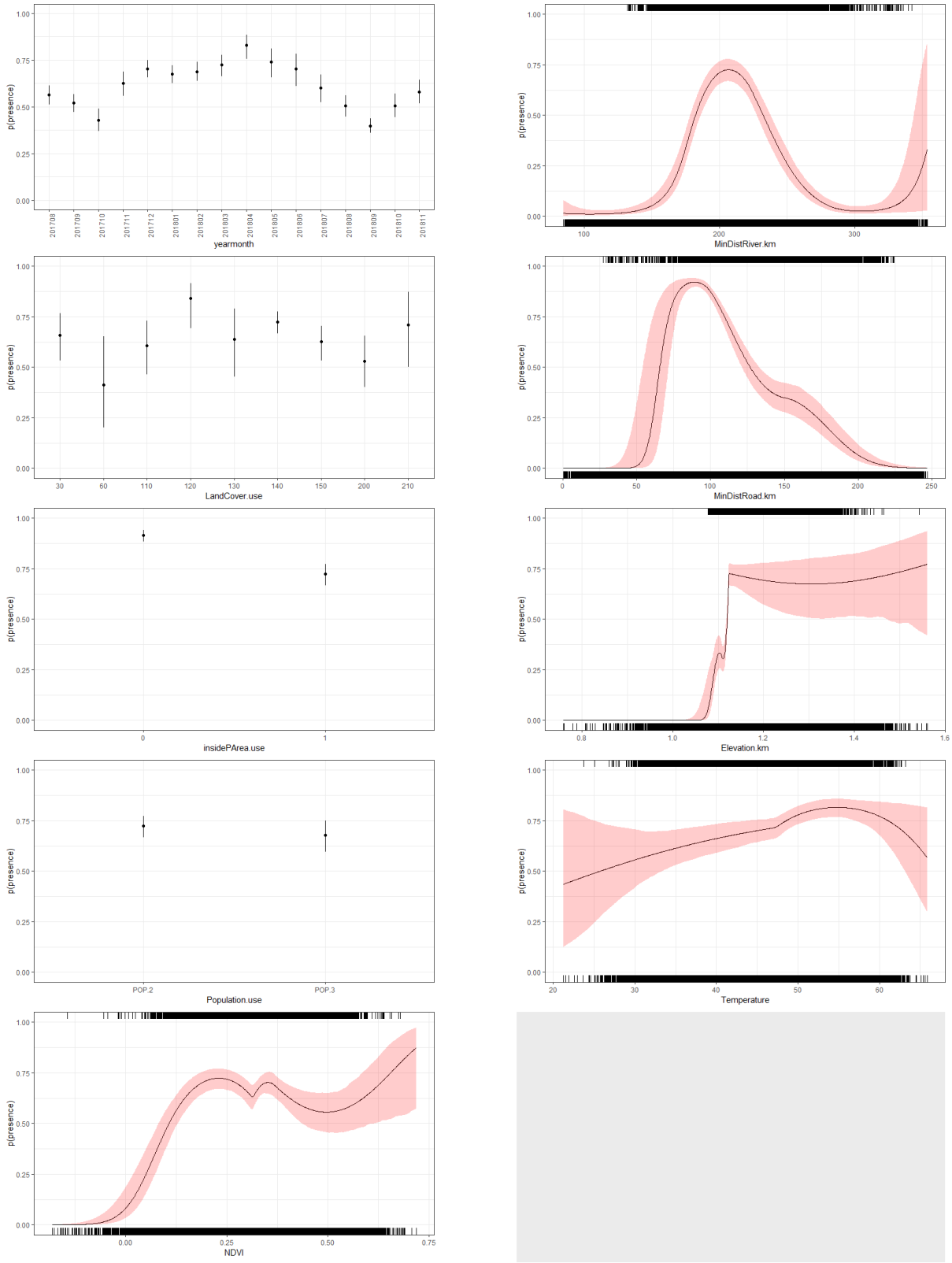

Figure VIII. 4 Functional response for each model covariate for bird 5785. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

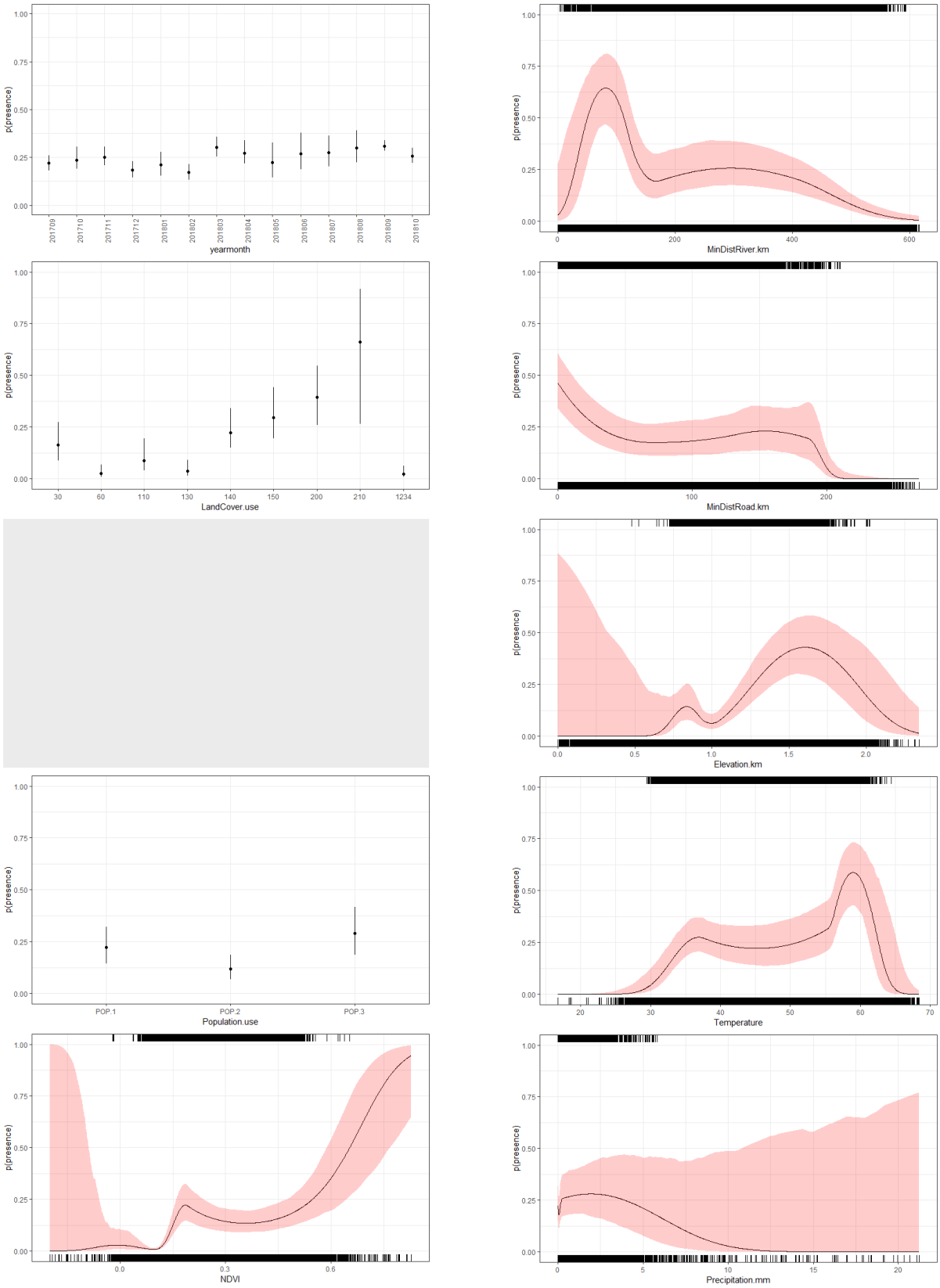

Figure VIII. 5 Functional response for each model covariate for bird 5786. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

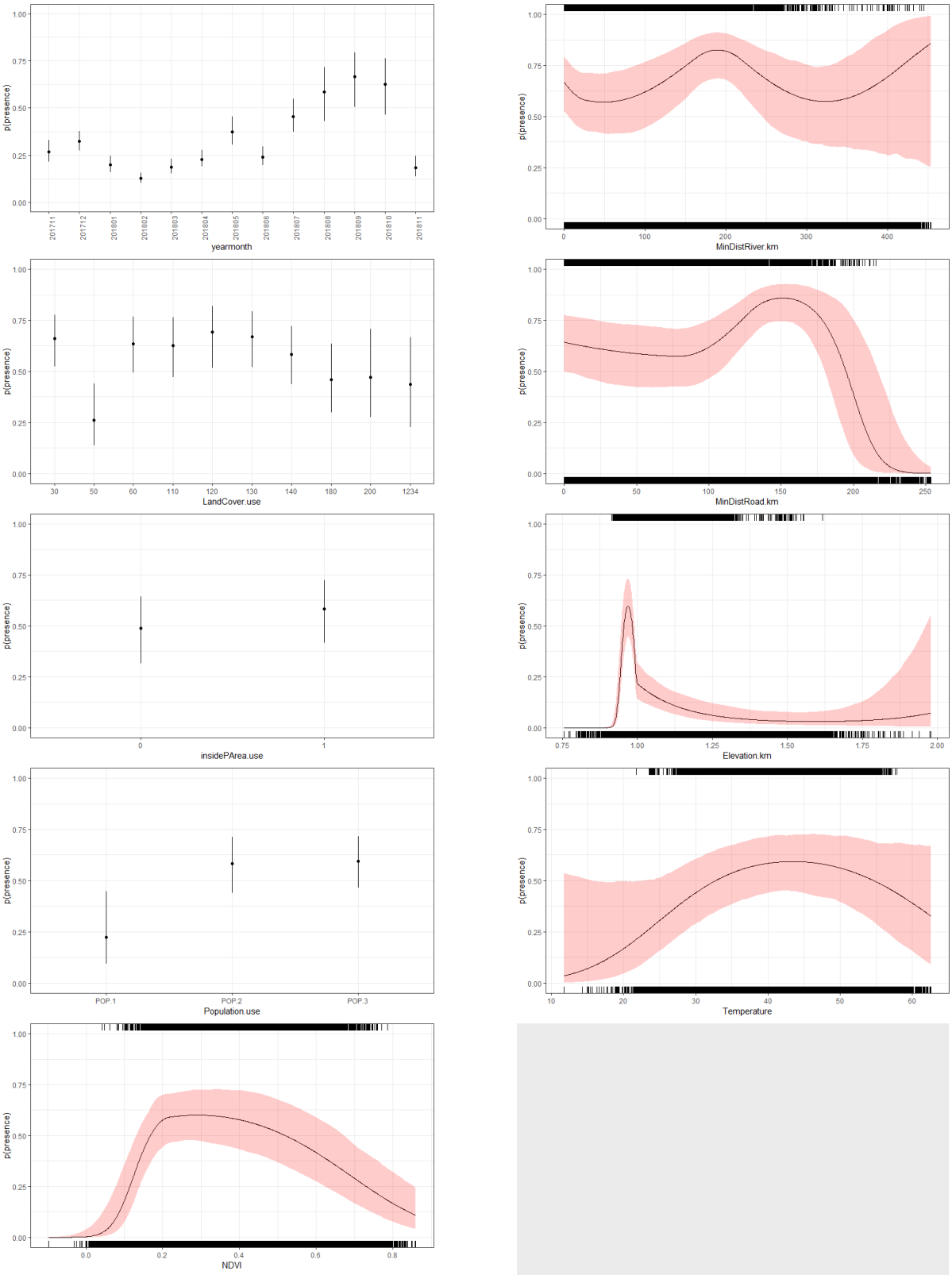

Figure VIII. 6 Functional response for each model covariate for bird 5787. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

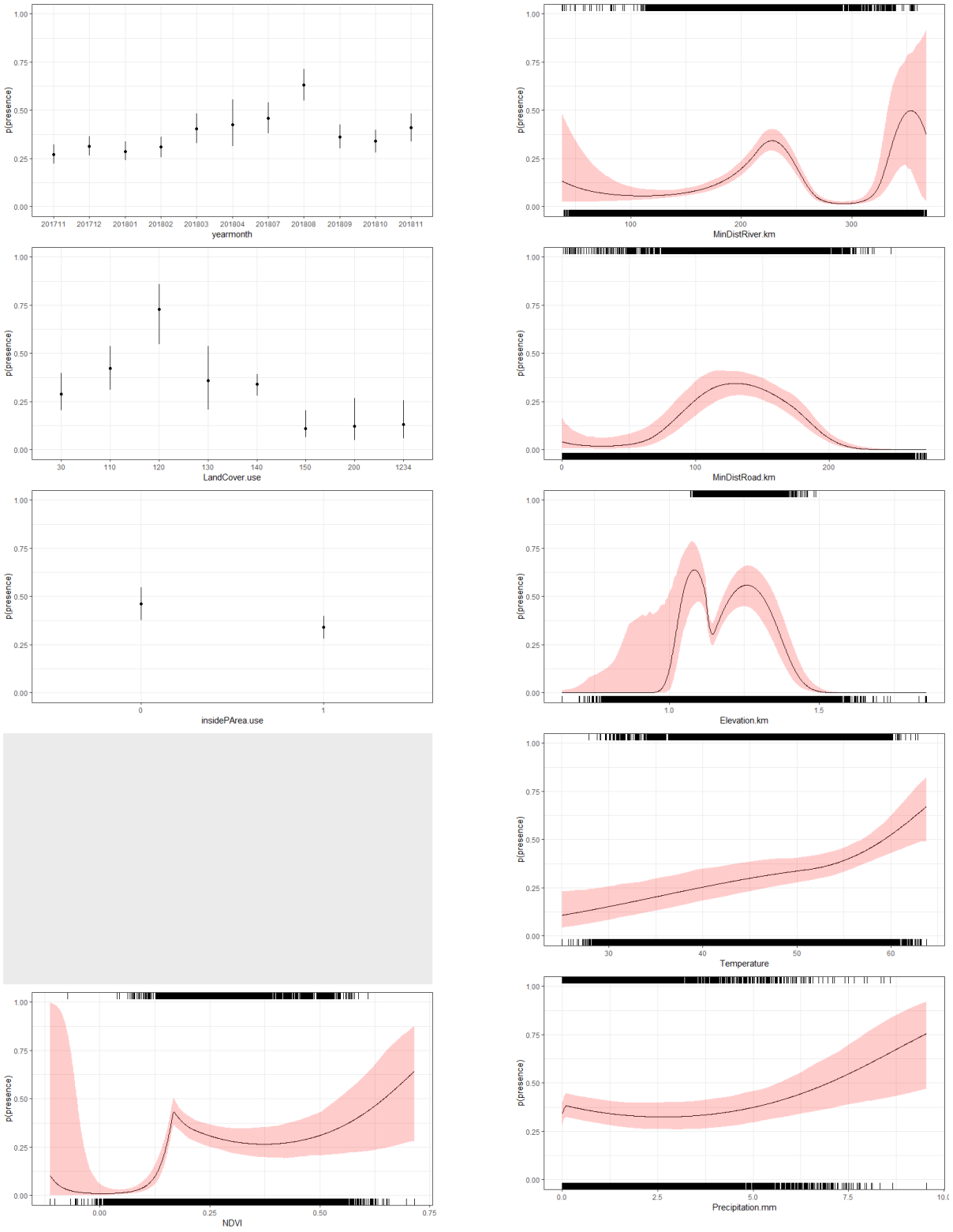

Figure VIII. 7 Functional response for each model covariate for bird 5788. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

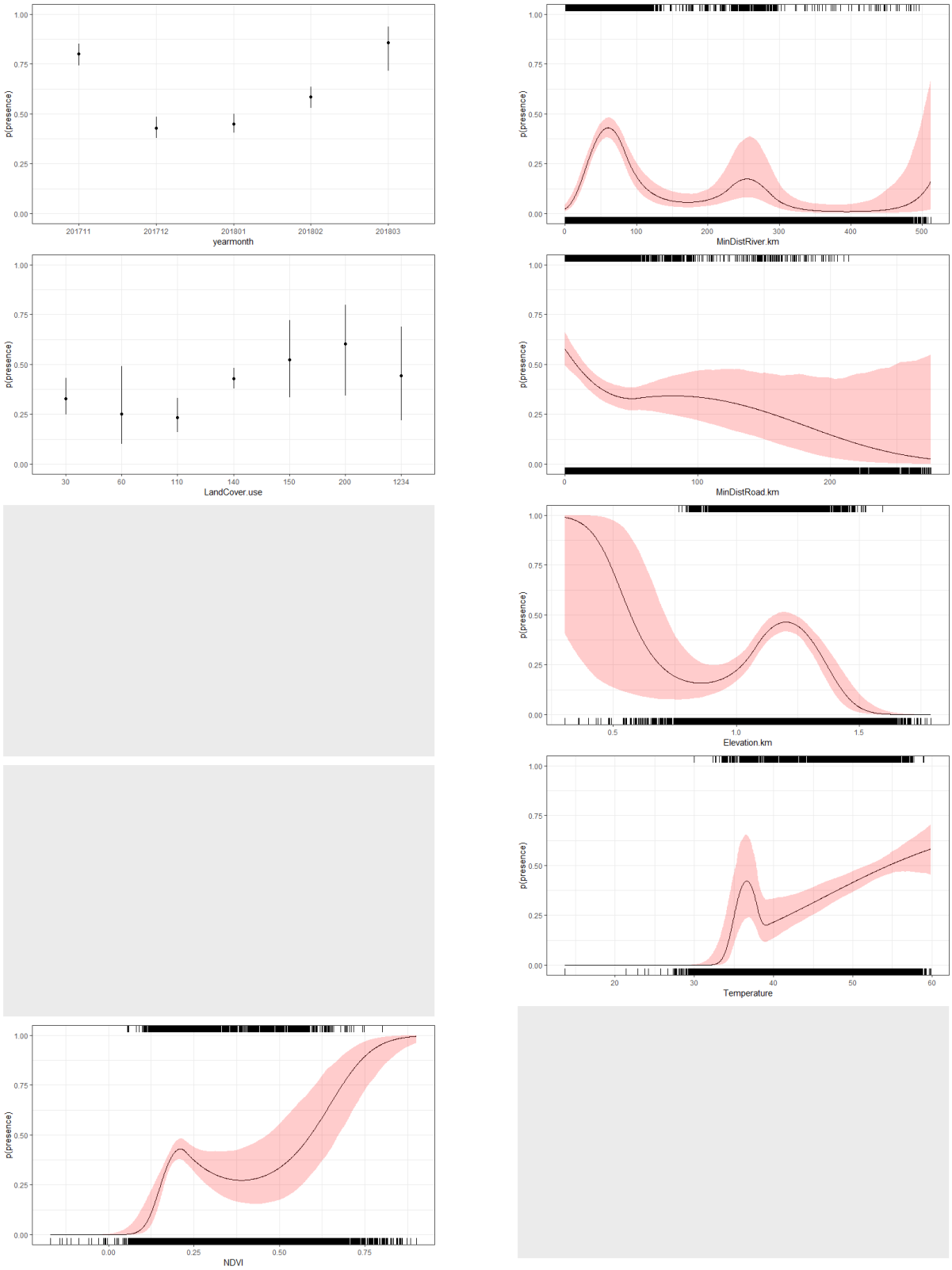

Figure VIII. 8 Functional response for each model covariate for bird 5789. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

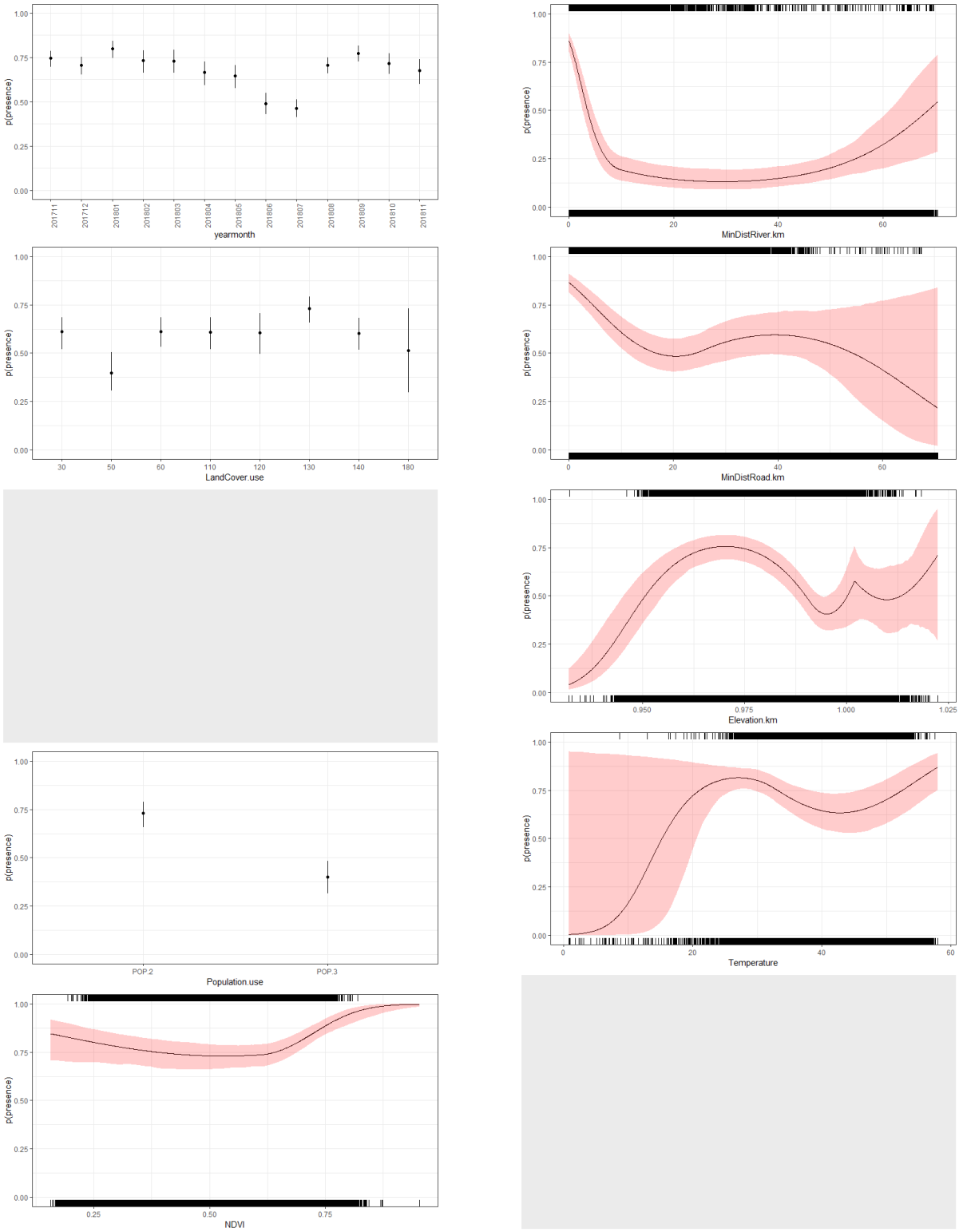

Figure VIII. 9 Functional response for each model covariate for bird CAT1. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

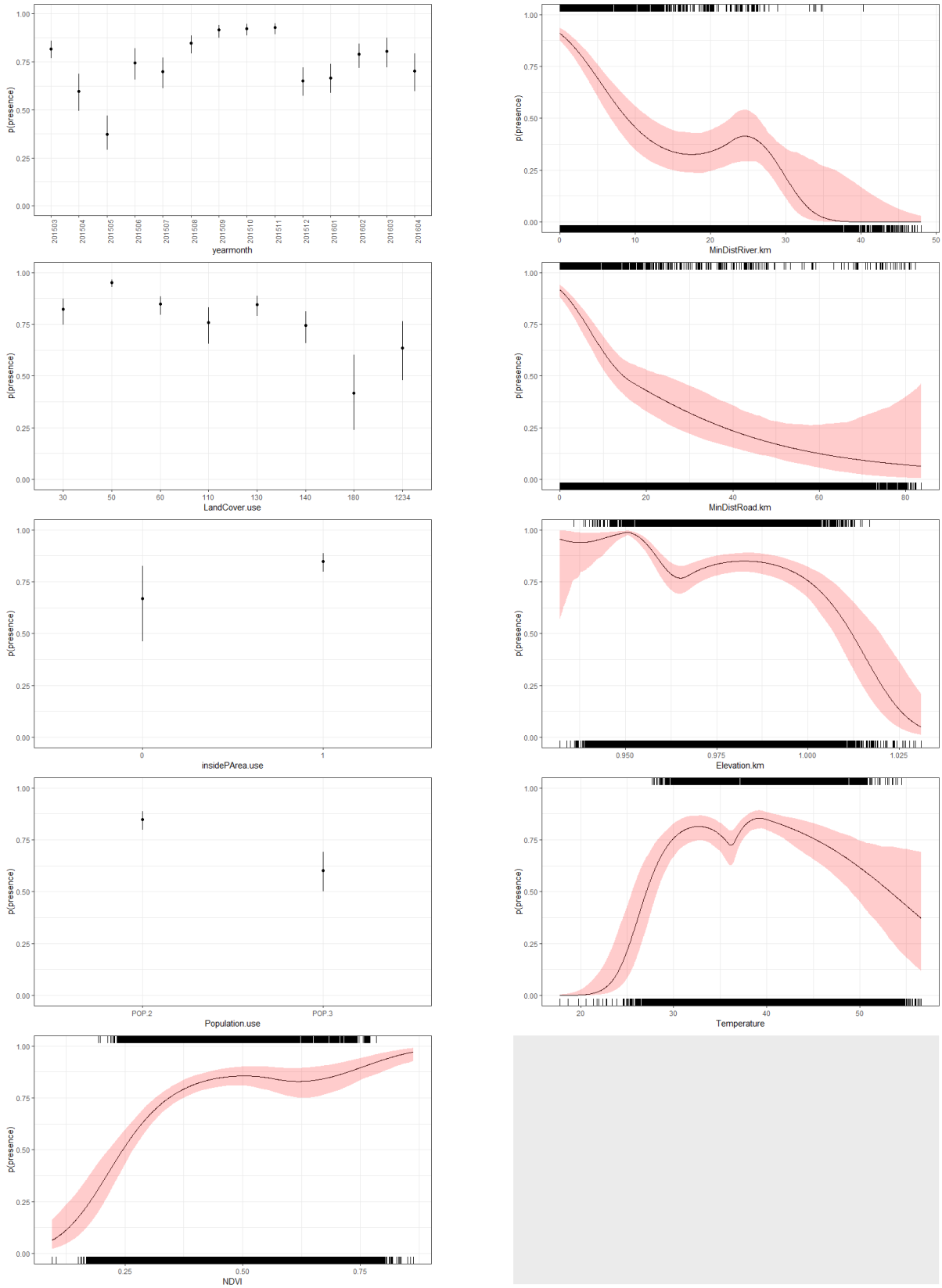

Figure VIII. 10 Functional response for each model covariate for bird st2010-1330. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

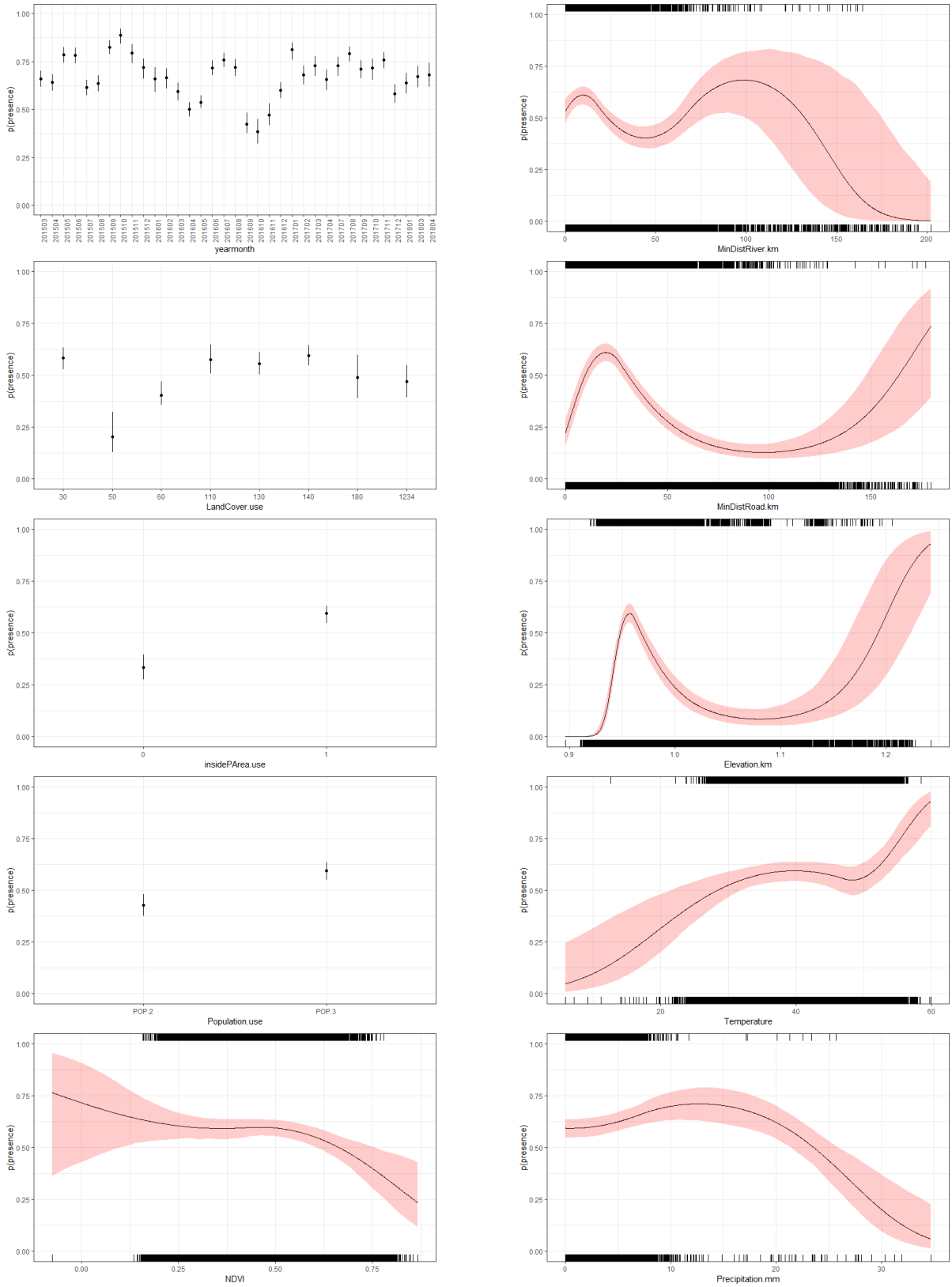

Figure VIII. 11 Functional response for each model covariate for bird st2010-1332. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

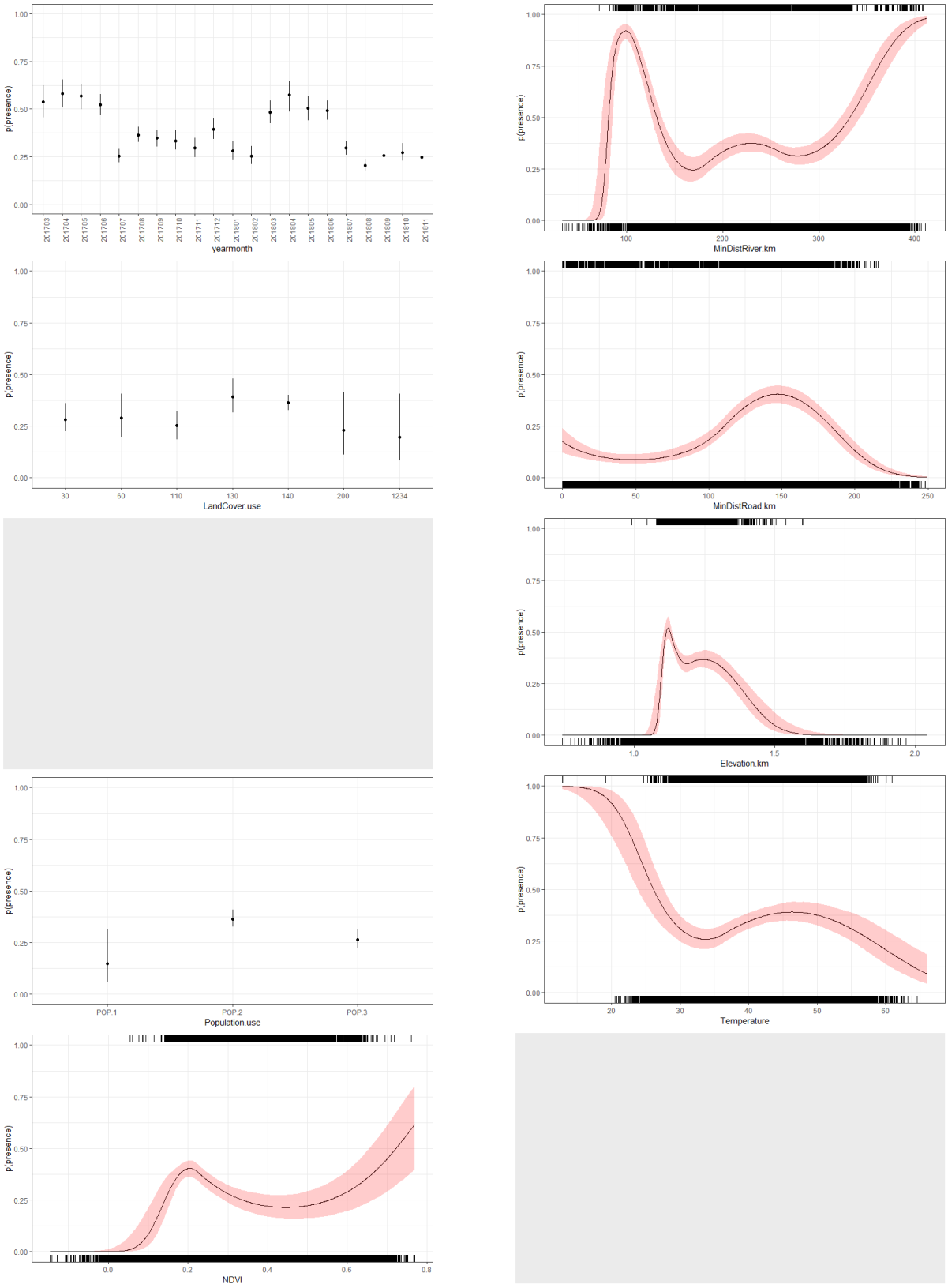

Figure VIII. 12 Functional response for each model covariate for bird st2010-2607. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

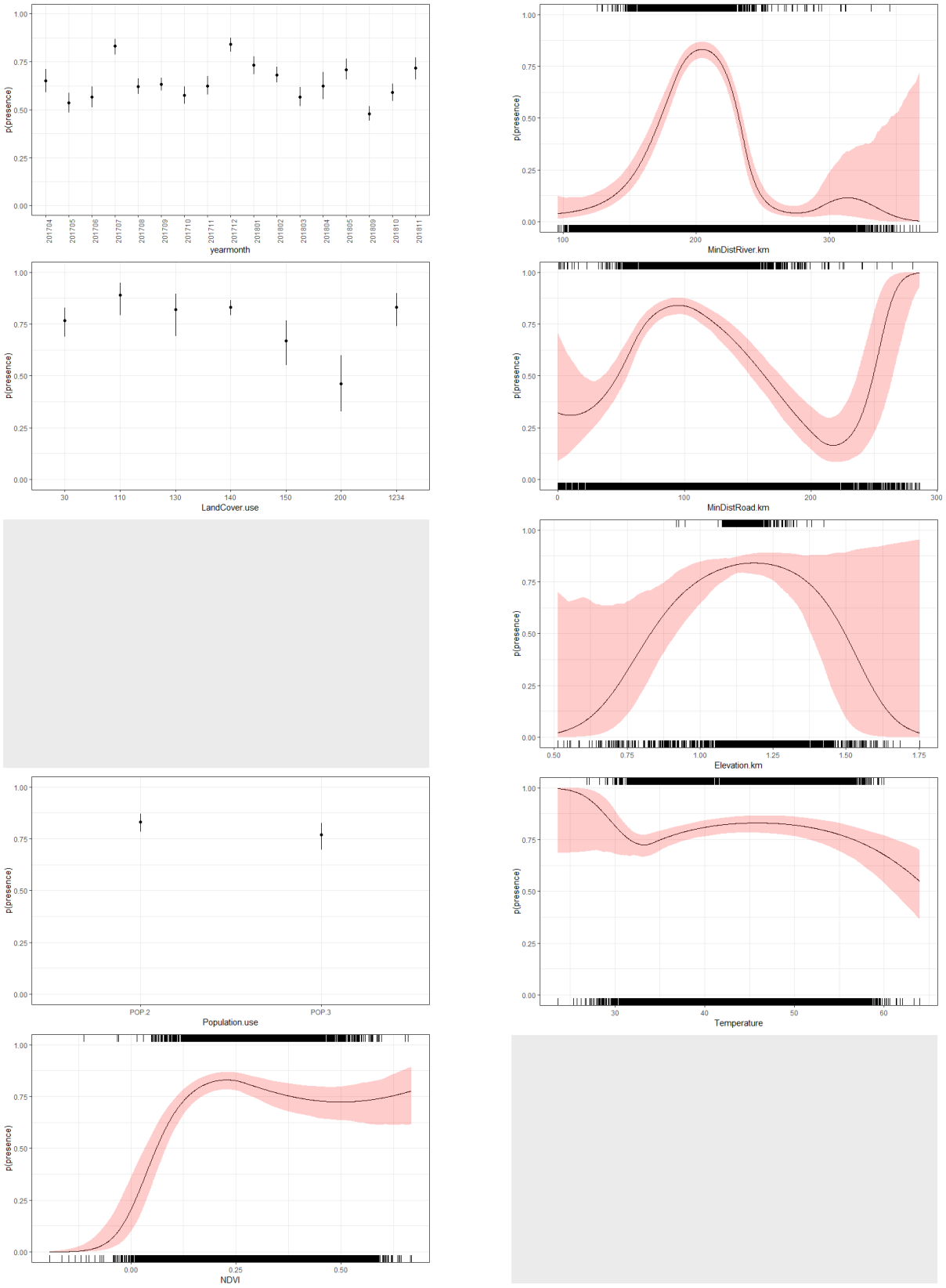

Figure VIII. 13 Functional response for each model covariate for bird st2010-2608. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

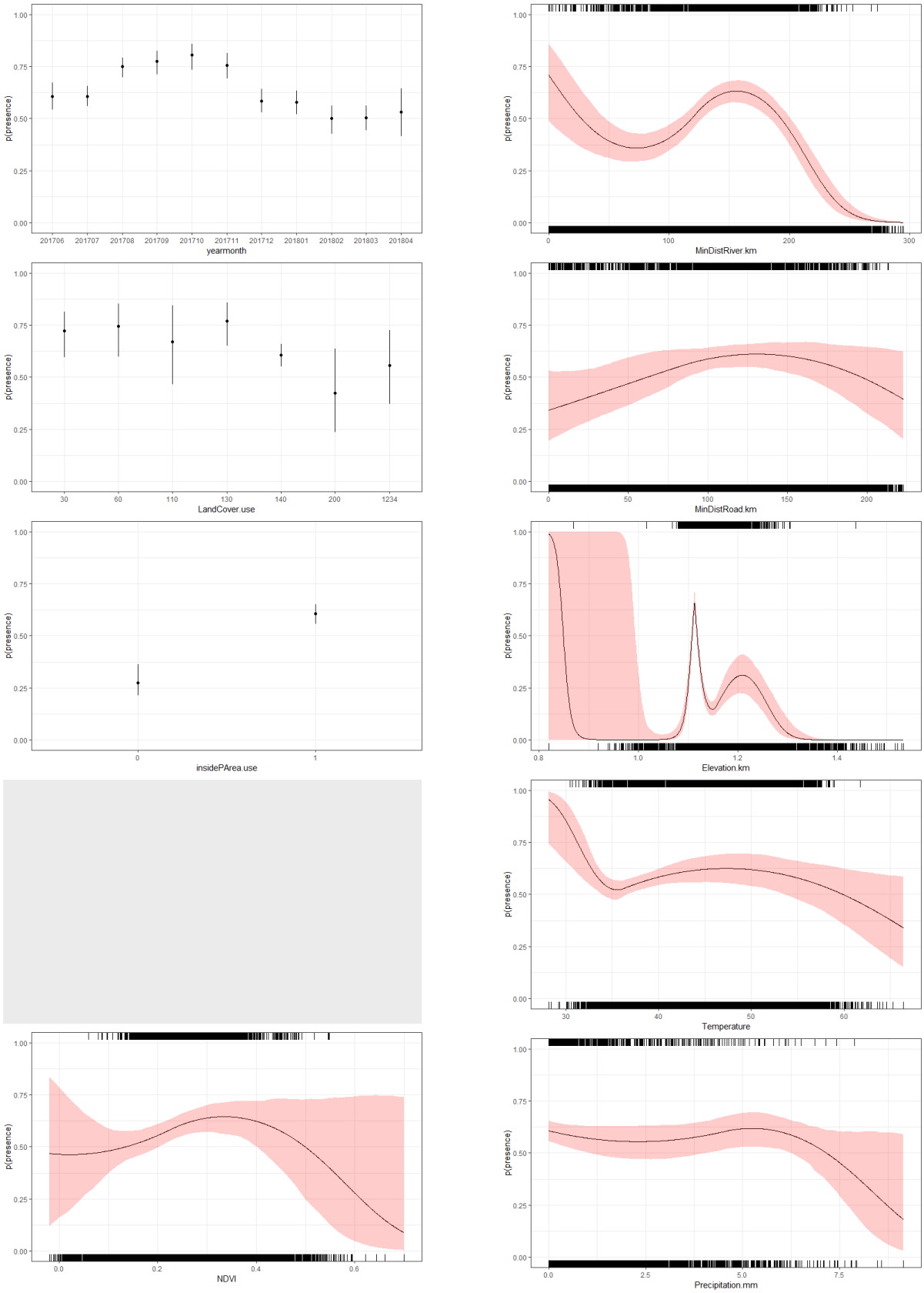

Figure VIII. 14 Functional response for each model covariate for bird st2010-2609. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

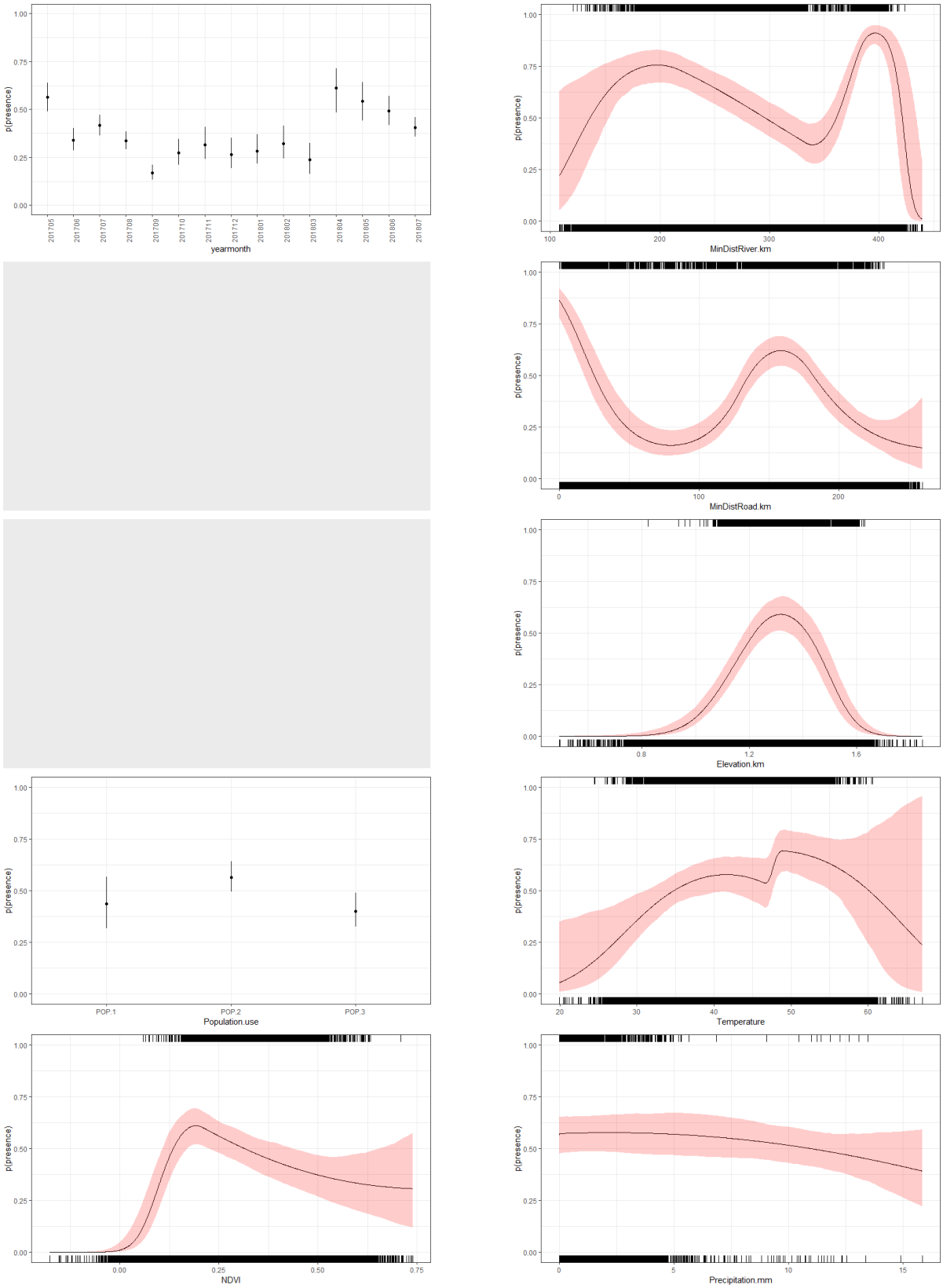

Figure VIII. 15 Functional response for each model covariate for bird st2010-2697. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

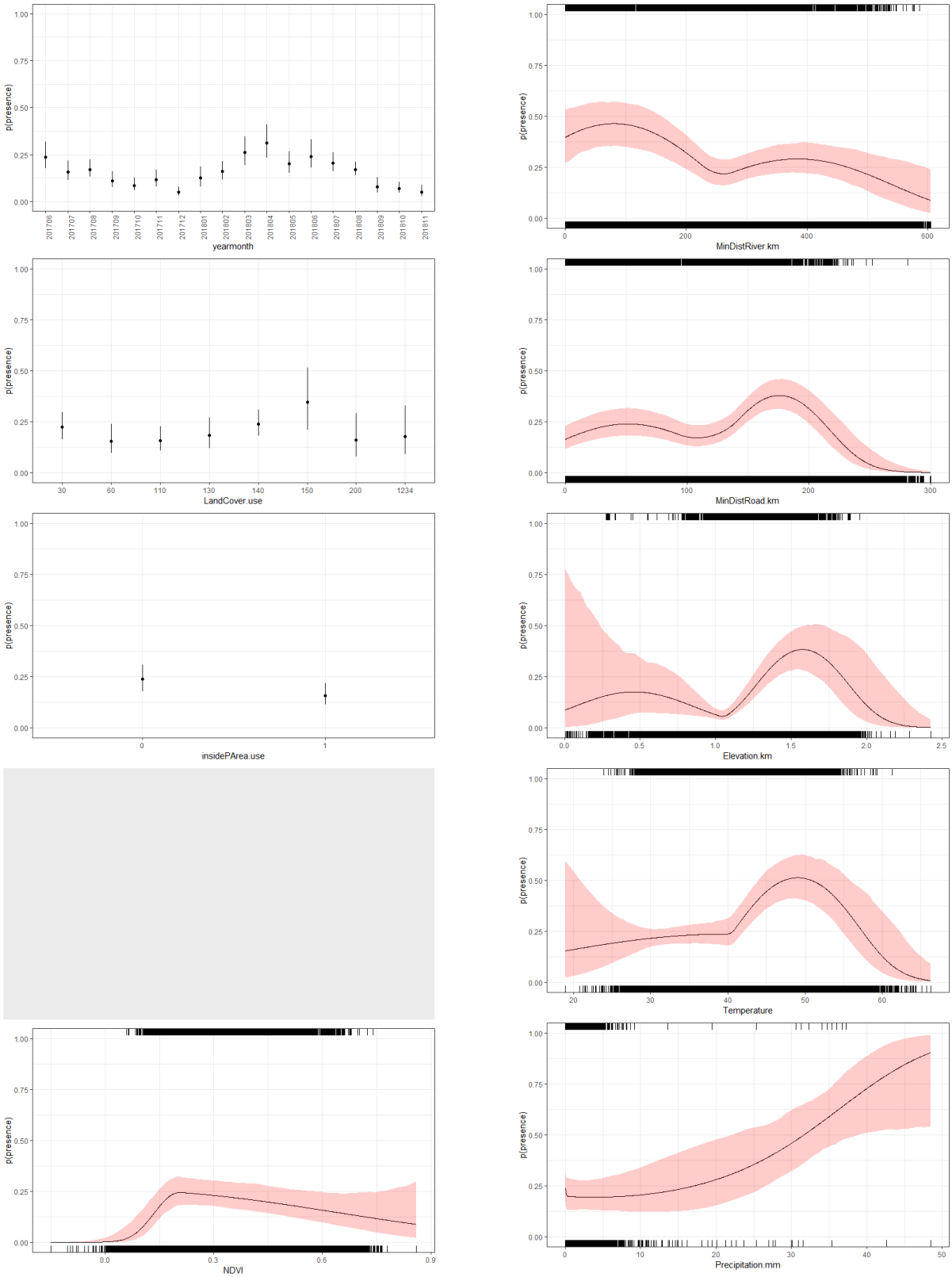

Figure VIII. 16 Functional response for each model covariate for bird st2010-2700. Plots in grey represent covariates that were excluded from the model. The tick marks on the top and bottom of each figure show the values of the covariate recorded in each vulture location (I.e., a presence, the 1's) and pseudo-absence (0's).

Appendix IX Habitat modelling: seasonal predictions for each vulture

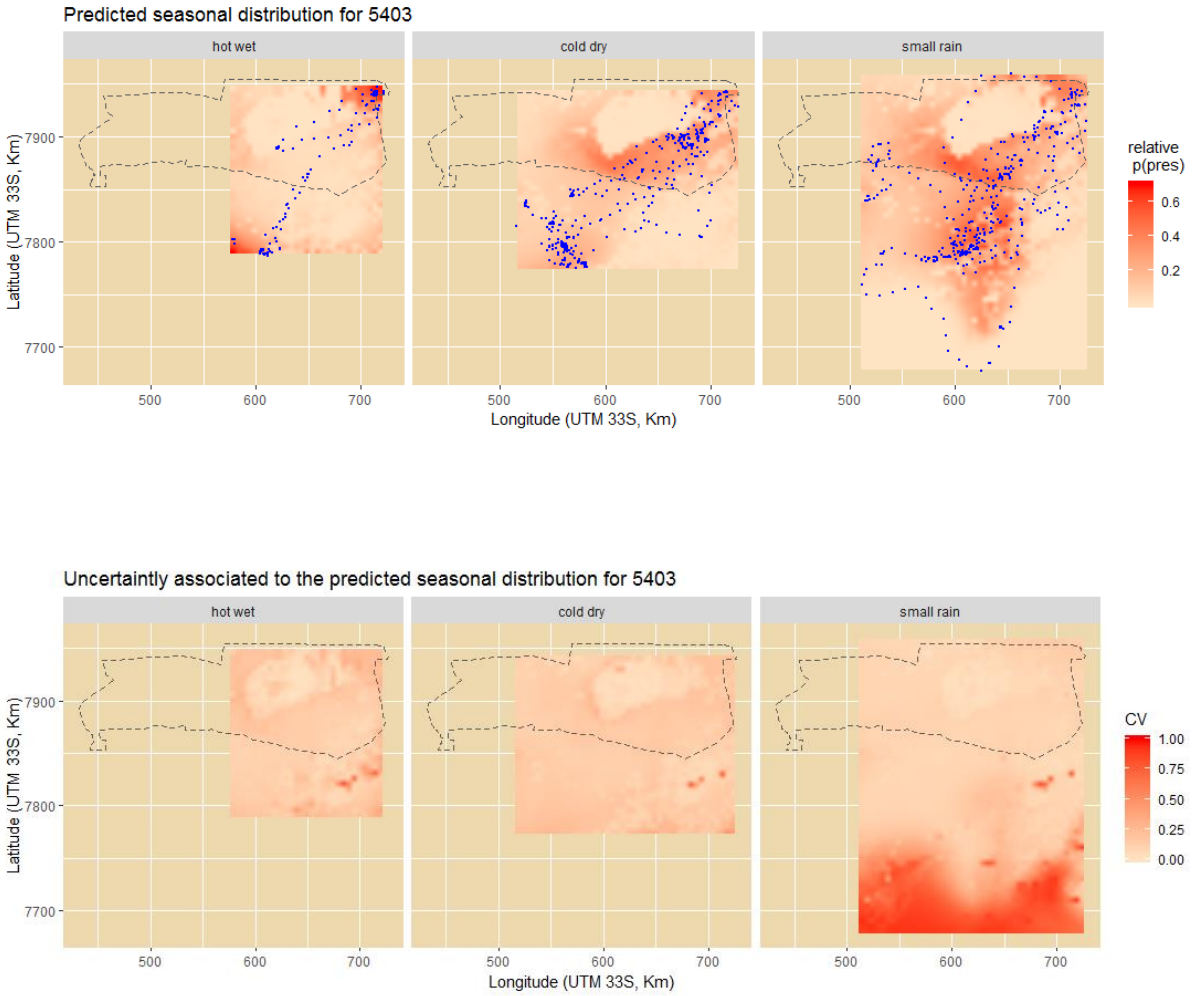

Figure IX. 1 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CVbound; bottom), illustrating the seasonal distribution for vulture 5403. Borders of Etosha National Park shown for reference.

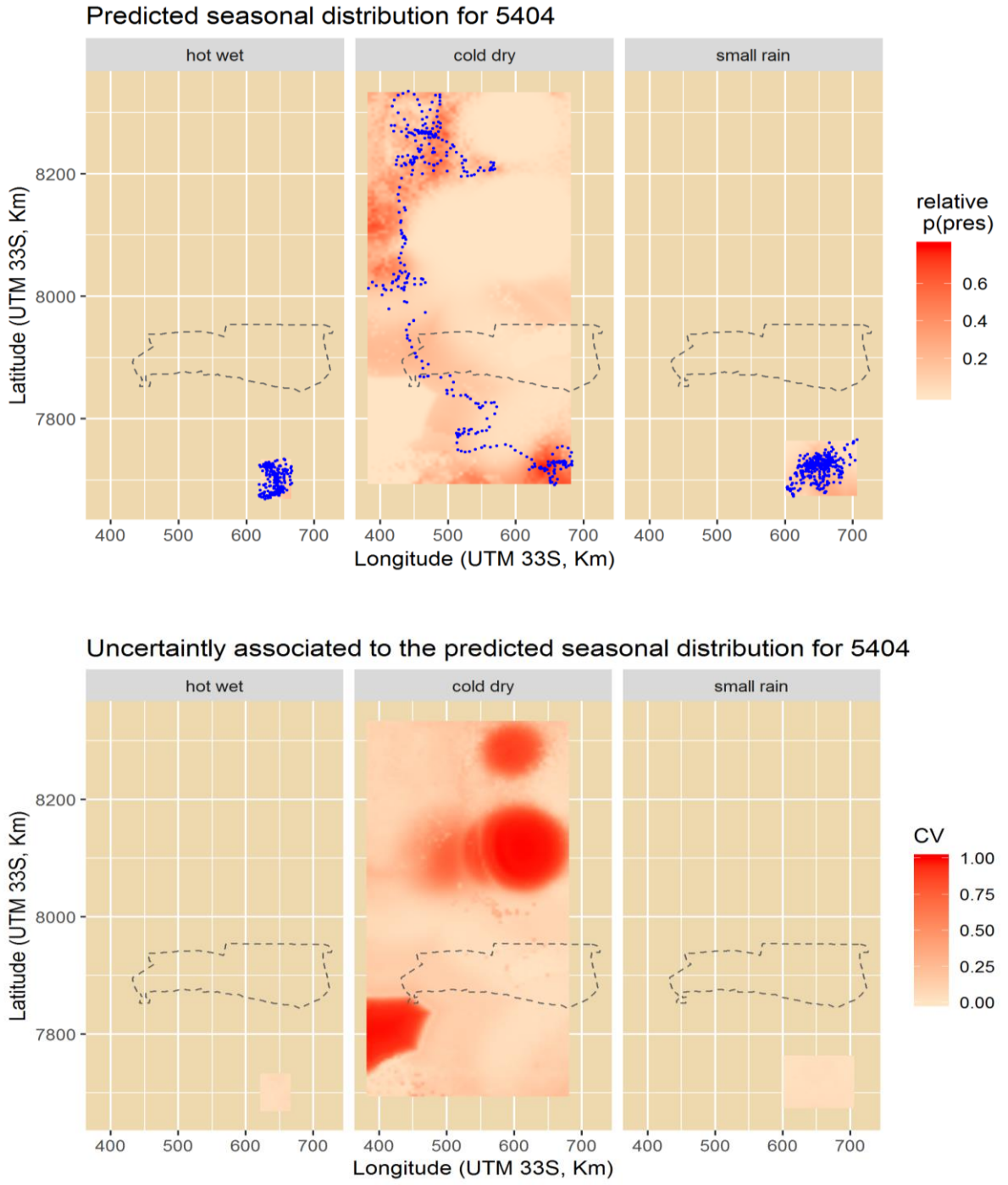

Figure IX. 2 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5404. Borders of Etosha National Park shown for reference.

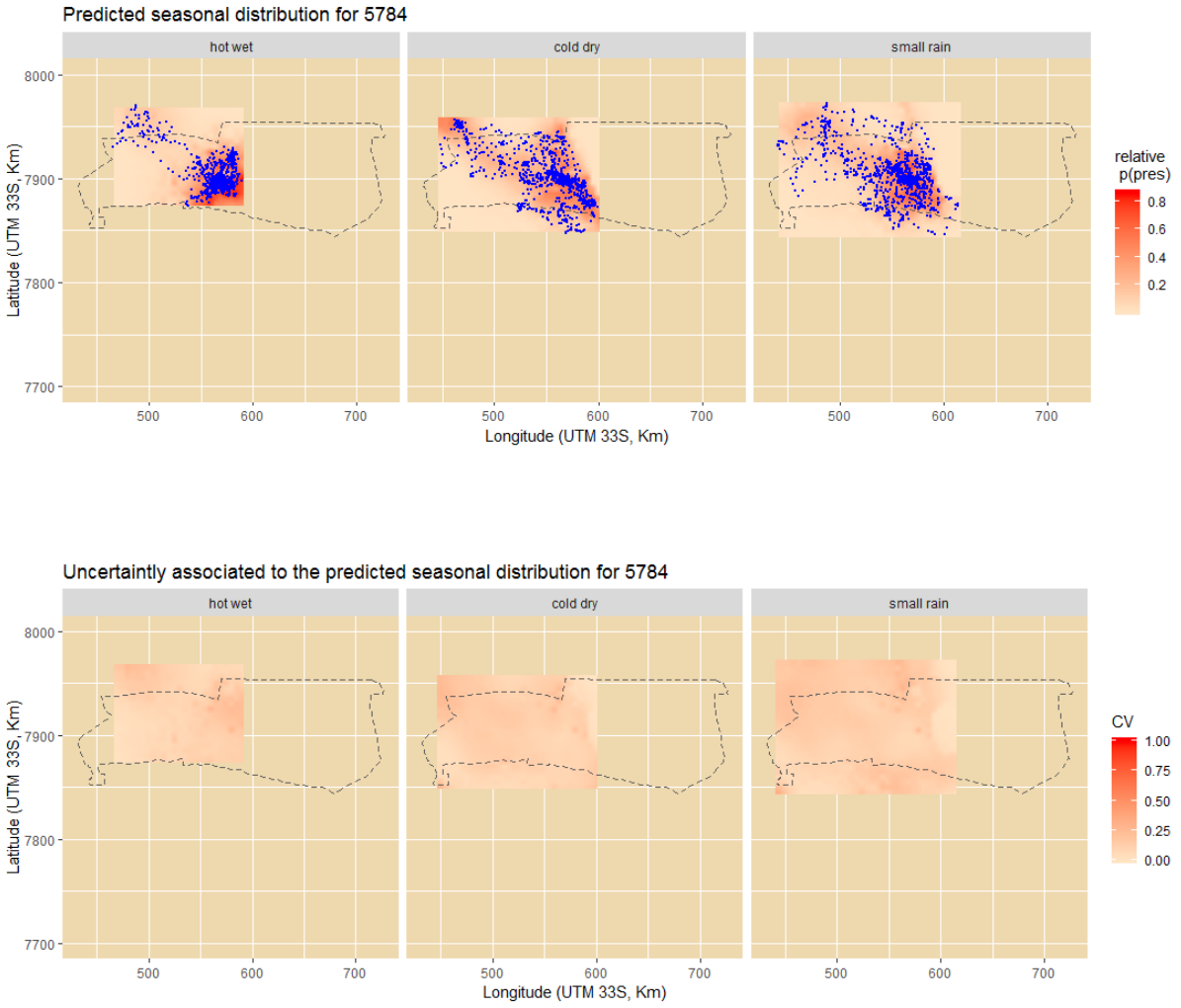

Figure IX. 3 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5784. Borders of Etosha National Park shown for reference.

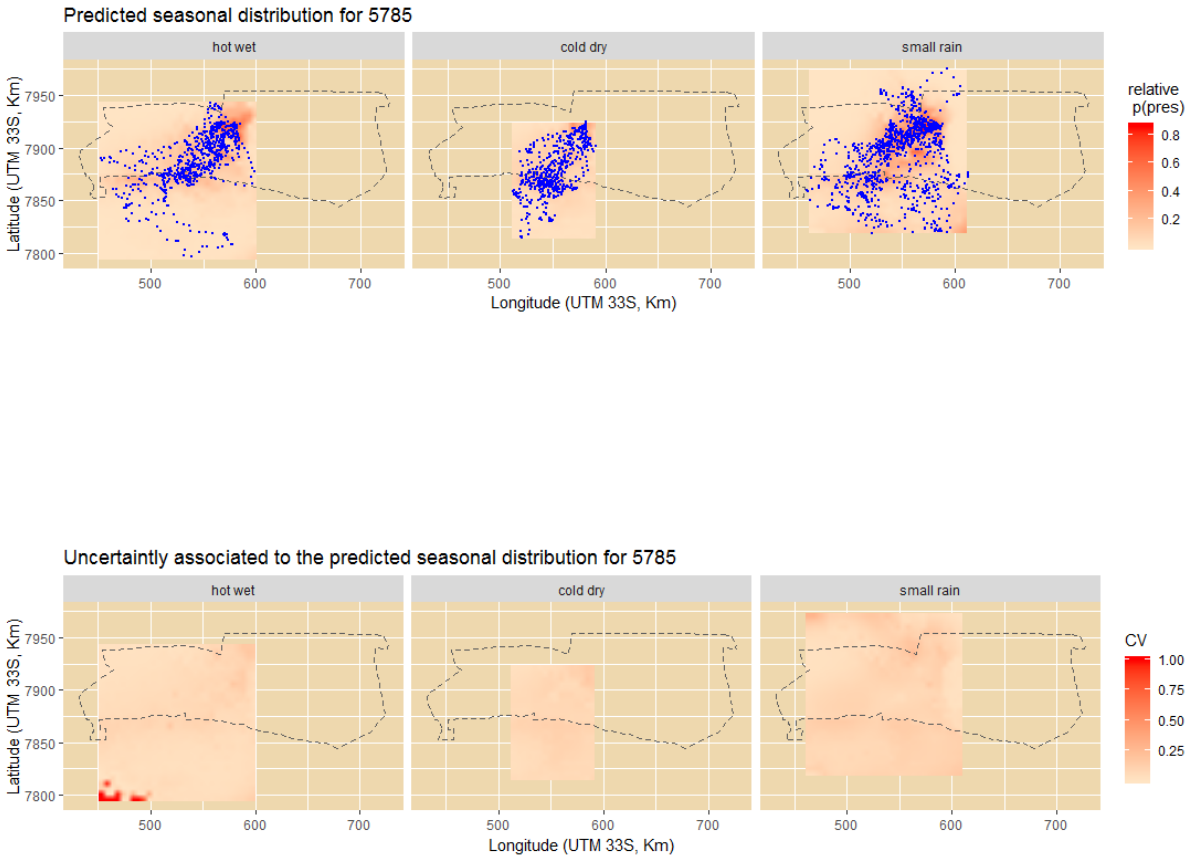

Figure IX. 4 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5785. Borders of Etosha National Park shown for reference.

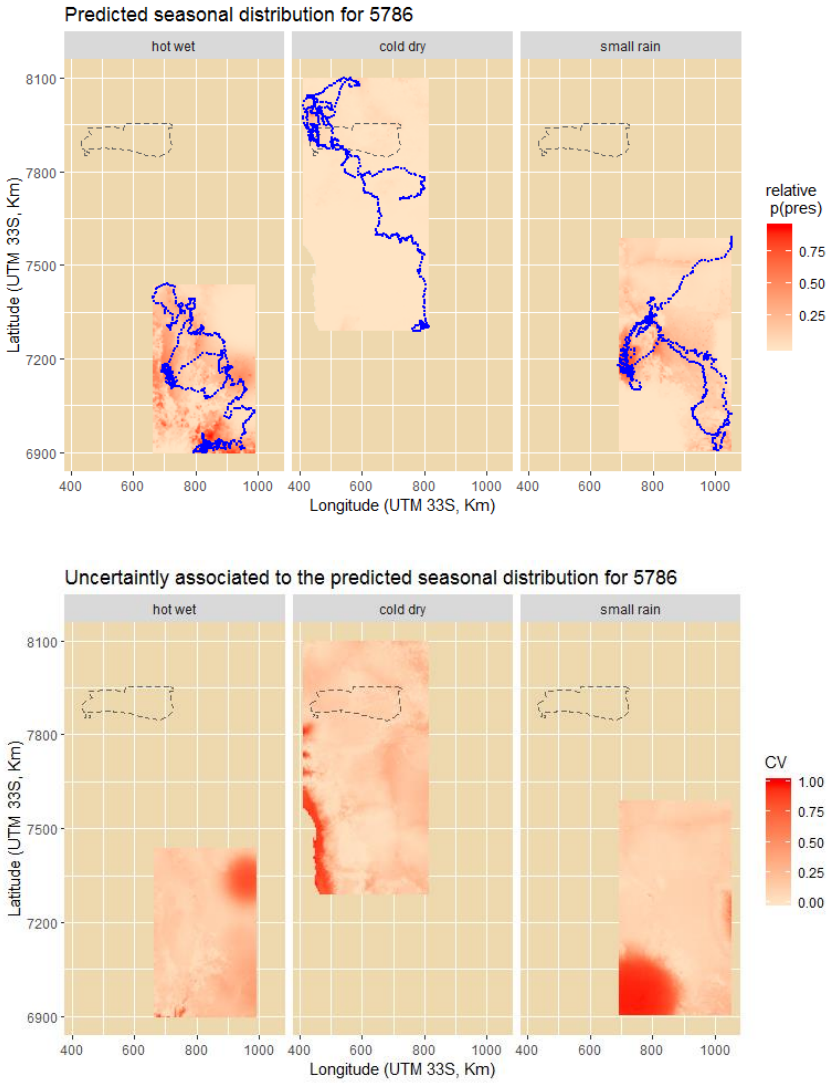

Figure IX. 5 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5786. Borders of Etosha National Park shown for reference.

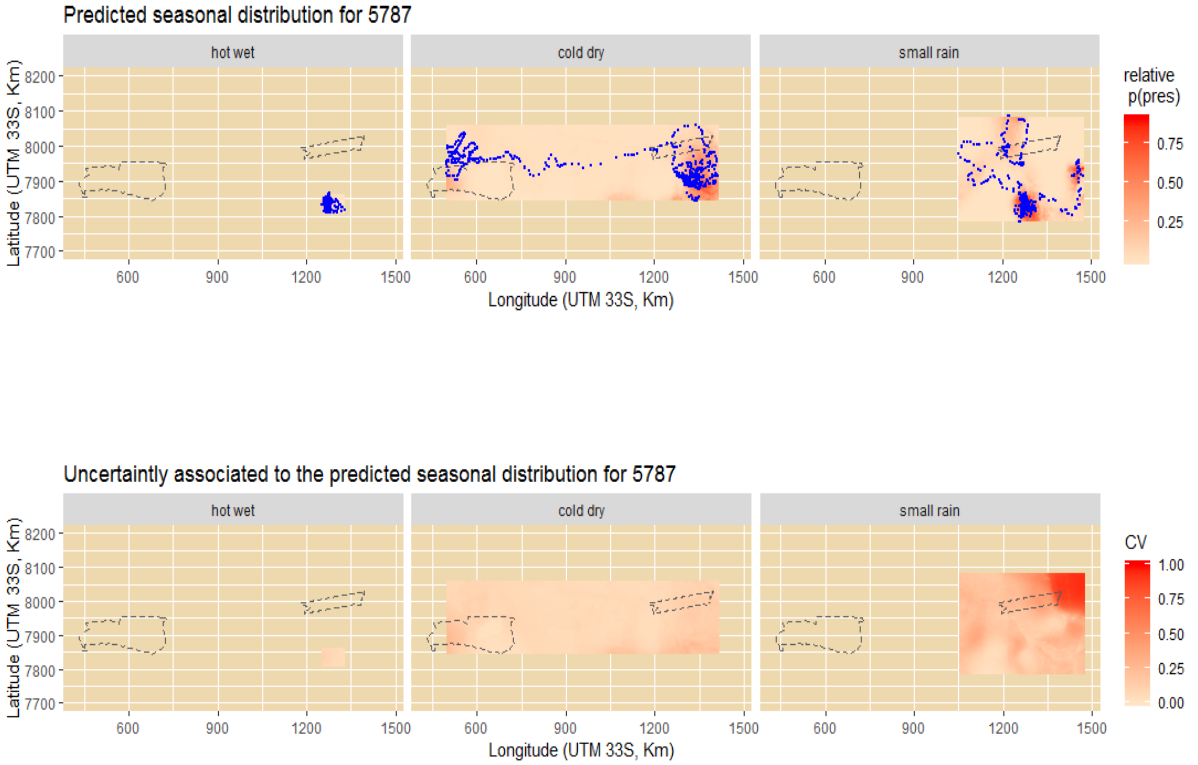

Figure IX. 6 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5403. Borders of both Etosha and Bwabwata National Parks are shown for reference.

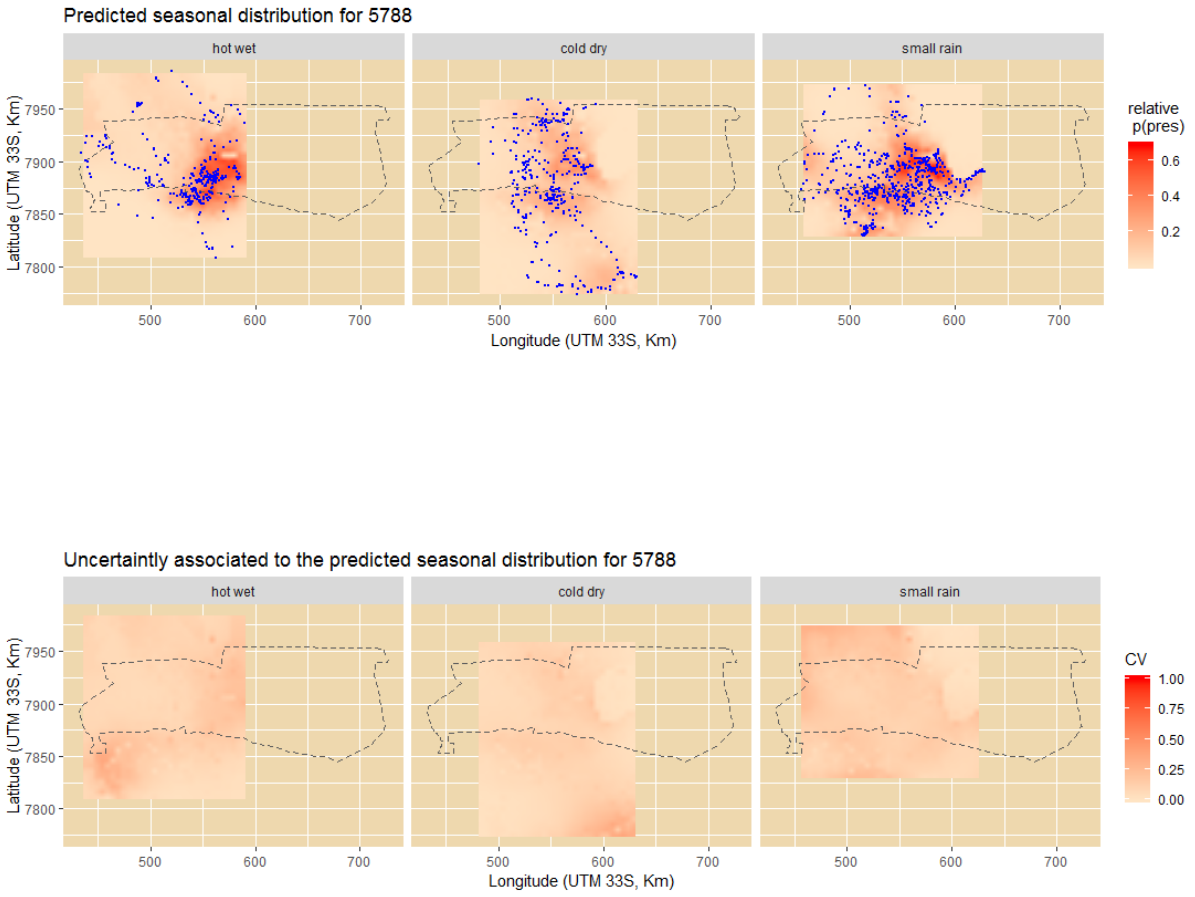

Figure IX. 7 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5788. Borders of Etosha National Park shown for reference.

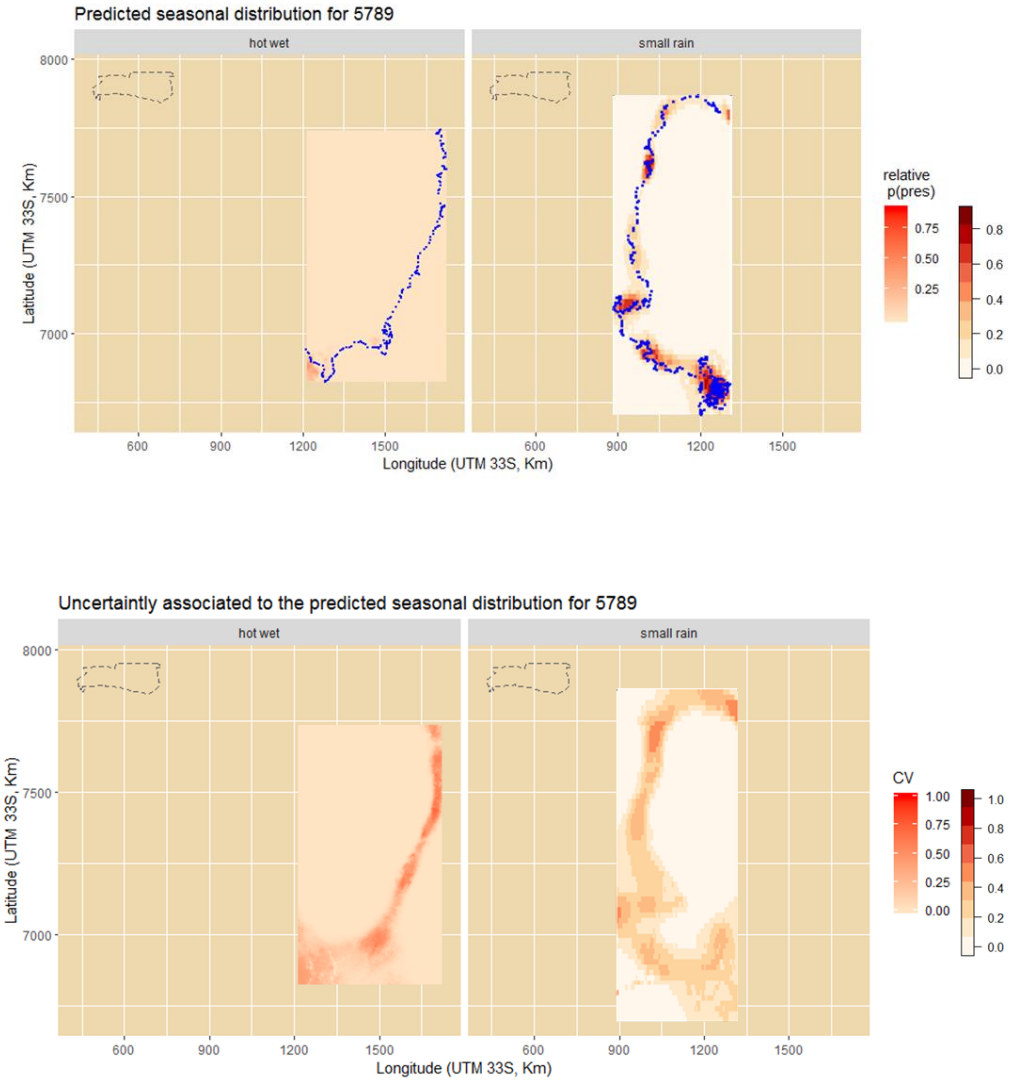

Figure IX. 8 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture 5789. Two scales are shown as a second plotting engine was necessary. Borders of Etosha National Park shown for reference.

Figure IX. 9 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture CAT1. Borders of Bwabwata National Park shown for reference.

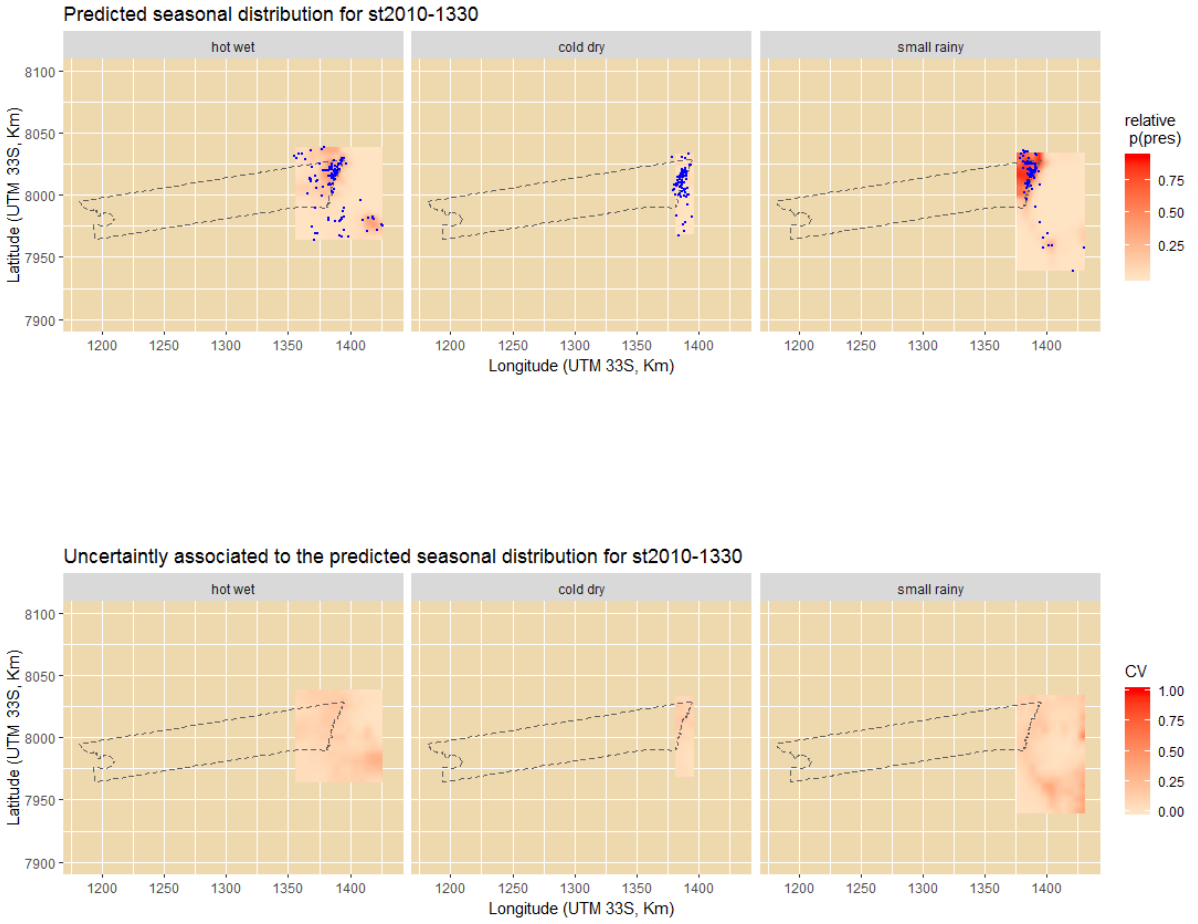

Figure IX. 10 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-1330. Borders of Bwabwata National Park shown for reference.

Figure IX. 11 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-1332. Borders of Bwabwata National Park shown for reference.

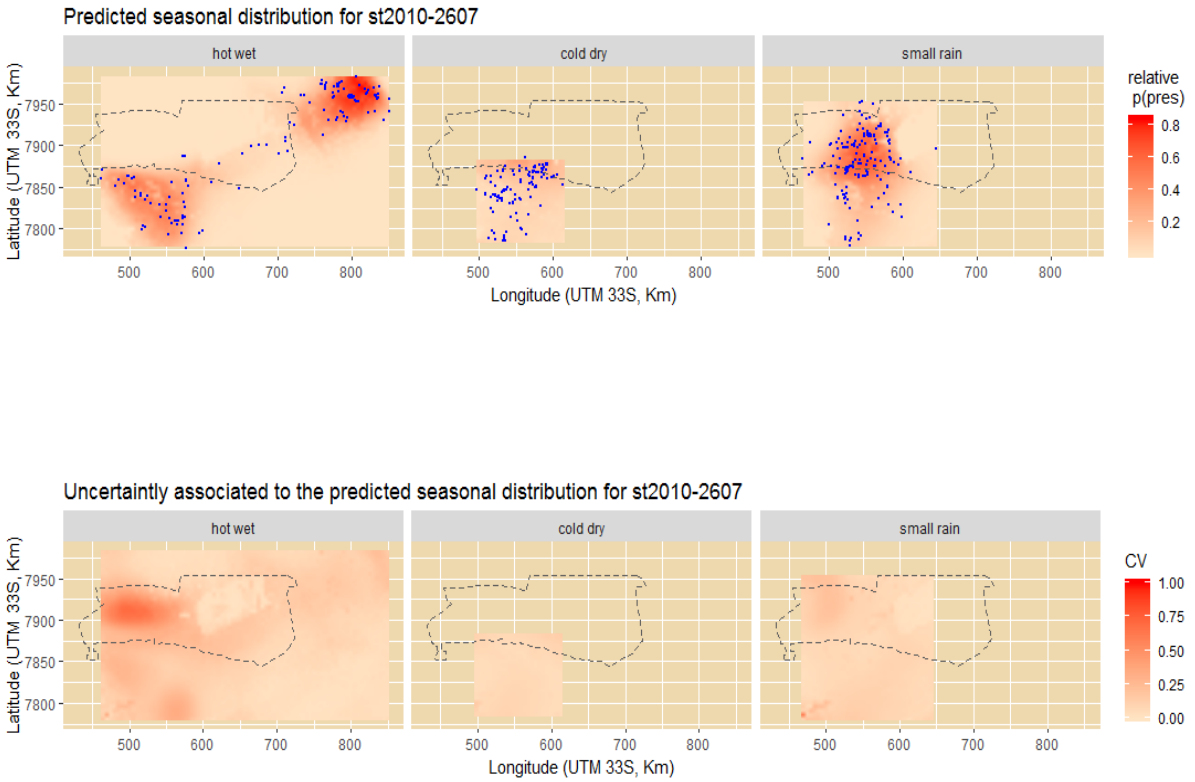

Figure IX. 12 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-2607. Borders of Etosha National Park shown for reference.

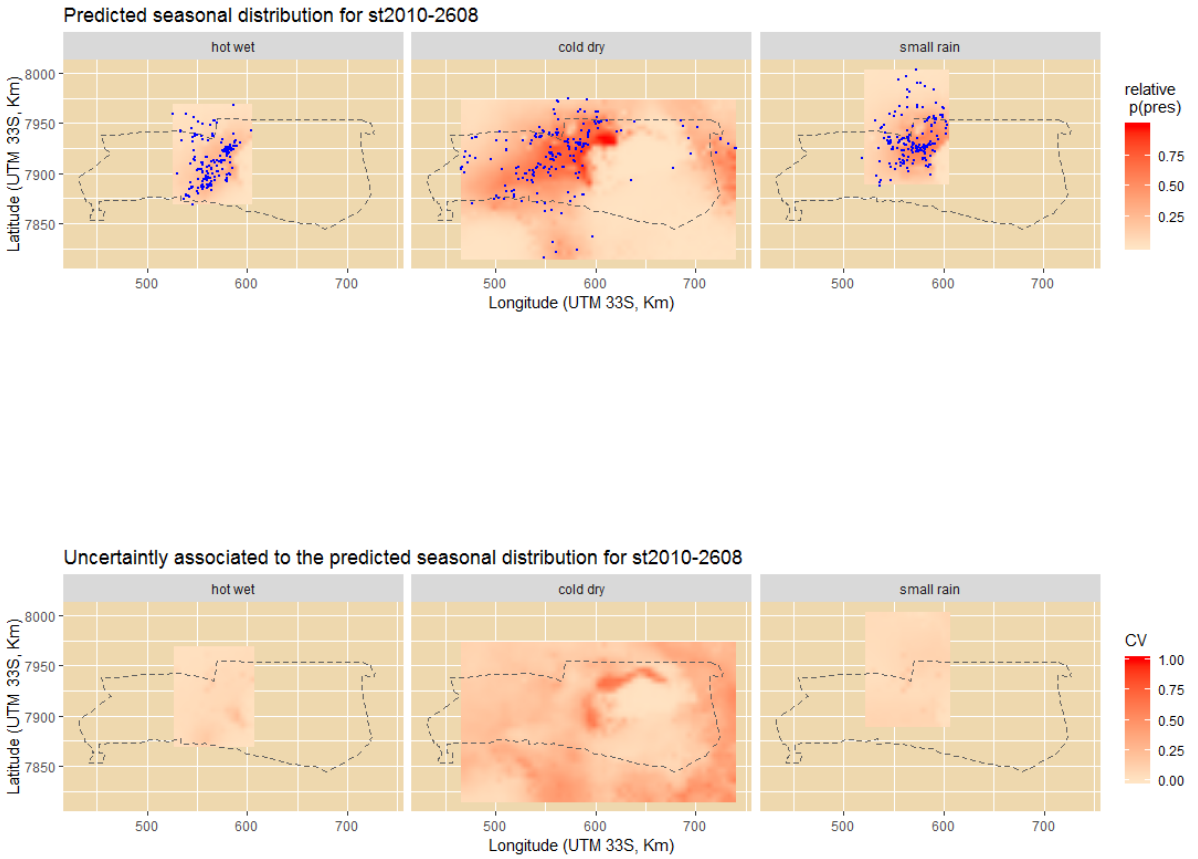

Figure IX. 13 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-2608. Borders of Etosha National Park shown for reference.

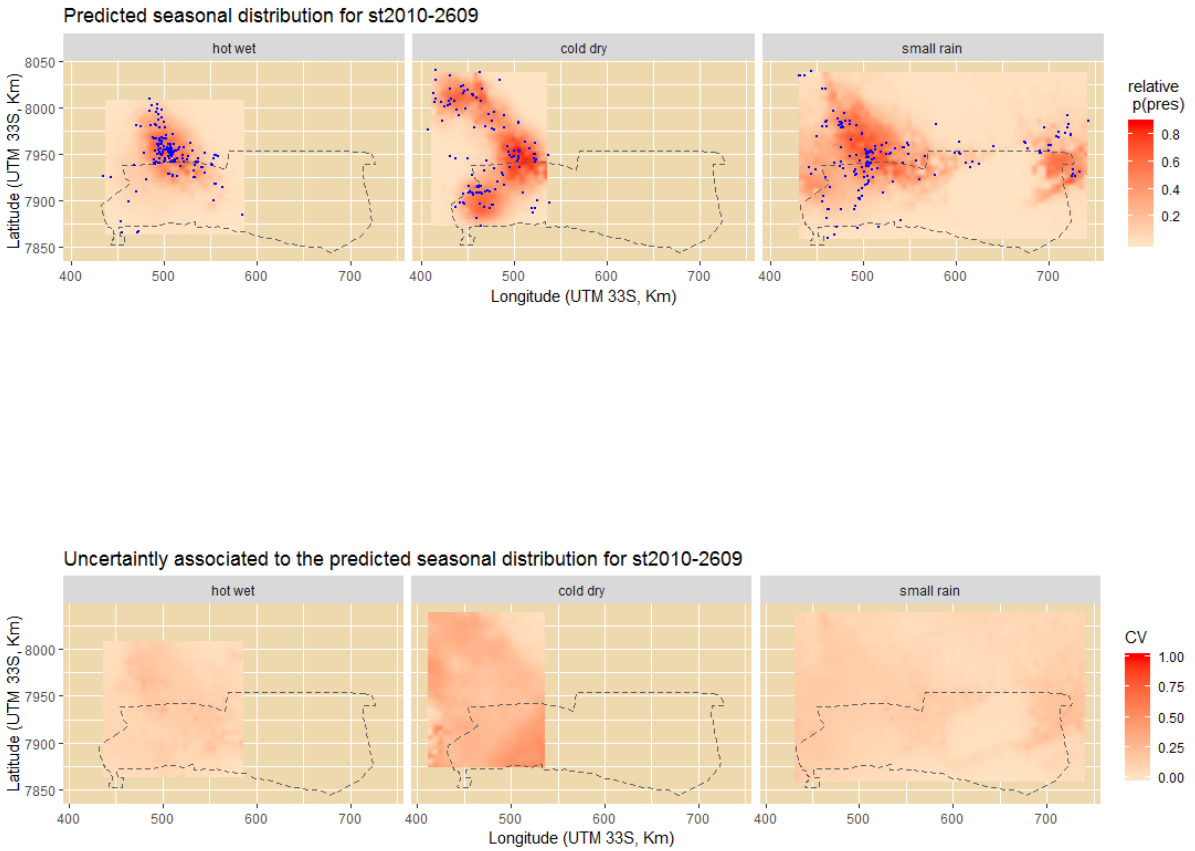

Figure IX. 14 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-2609. Borders of Etosha National Park shown for reference.

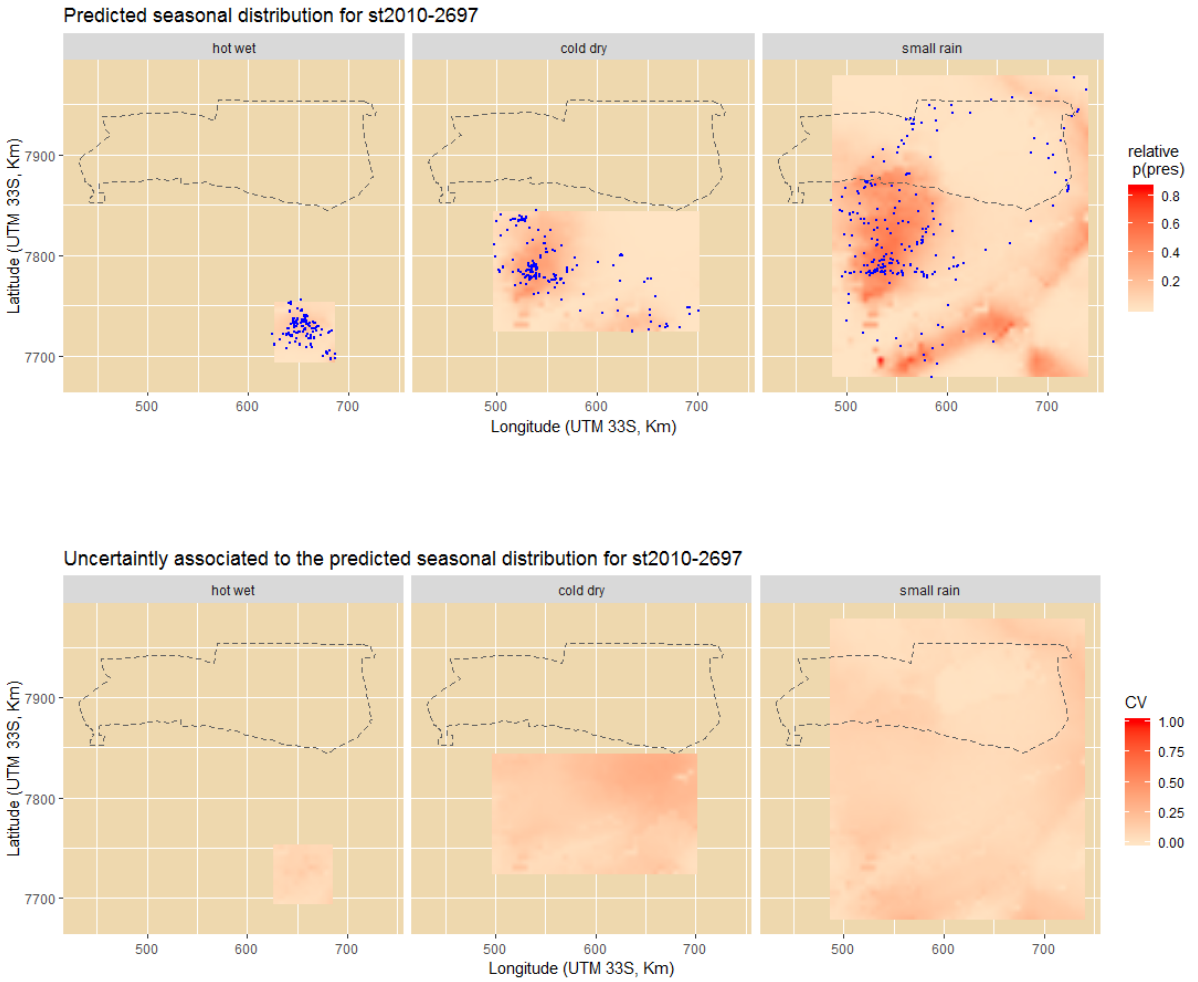

Figure IX. 15 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-2697. Borders of Etosha National Park shown for reference.

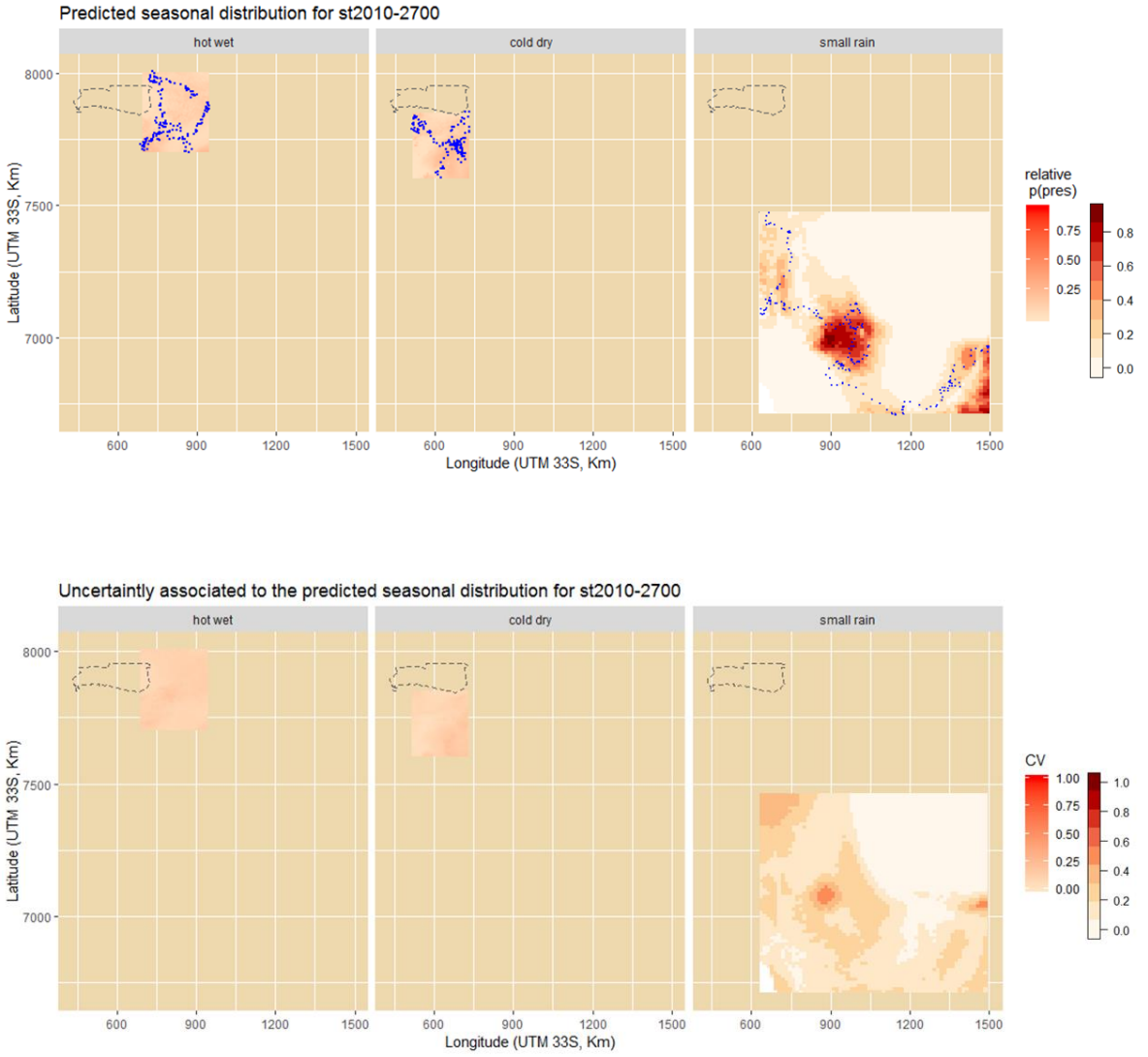

Figure IX. 16 Maps of predicted relative probability presence (GPS locations shown in blue; top) with associated uncertainty (Coefficient of Variation, CV_{bound}; bottom), illustrating the seasonal distribution for vulture st2010-2700. Two scales are shown as a second plotting engine was necessary. Borders of Etosha National Park shown for reference.